EVALUATION OF GROWTH AND MIGRATION TRENDS ON THE SURVIVAL AND RECRUITMENT OF CHINOOK SALMON IN SOUTHEASTERN ALASKA RIVERS

By

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Abstract

Highly variable recruitment and declines in productivity and abundance of Chinook Salmon *Oncorhynchus tshawytscha* have created economic and cultural hardships for communities throughout Alaska. Although pre- and post-smolt growth are important for determining brood-year (BY) survival and productivity for Pacific salmon through size-mediated mortality, these relationships remain unclear for Chinook Salmon. As a result, it is necessary to better understand the relationships between environmental and biological factors that influence freshwater and marine growth, smolt outmigrations, and recruitment success. This study used retrospective growth to identify the importance of annual growth in determining BY survival and recruitment, determine if growth dependency between growth zones was present, and examine growth differences among age classes for Chinook Salmon in the Chilkat (BYs 1985 – 2007) and Stikine (BYs 1991 – 1998 and 2000 – 2007) rivers. Biological and environmental factors were also assessed to determine their influence on freshwater smolt production, smolt outmigration, and marine survival. Greater first-year marine growth was correlated with higher BY total return and productivity for Chinook Salmon from the Chilkat River and higher BY marine survival for Chinook Salmon from the Stikine River. Daily smolt outmigration of Chilkat River Chinook Salmon was positively correlated to water temperature and negatively correlated to discharge (Deviance explained = 68.5%), while timing of the start of outmigration was influenced by nearshore sea surface temperatures ($R^2 = 0.57$) and timing of the mid and end points were positively related to smolt length ($R^2 = 0.72$ and 0.34, respectively). Freshwater smolt production was negatively correlated to parr length and fall discharge and positively correlated to spring temperature and discharge ($R^2_{adj}= 0.52$). Marine survival of Stikine River Chinook Salmon was significantly related to smolt size ($R^2 = 0.26$), while Chilkat River Chinook Salmon were positively related to migration timing and smolt length and negatively related to discharge ($R^2 = 0.5$). These results support the importance of the early marine period in determining year-class strength and highlight the variation in mechanisms that influence recruitment success of Chinook Salmon stocks.

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General Introduction

Growth is an important factor influencing the survival and productivity of fishes (Healey 1982; Quinn 2005; Ruggerone et al. 2009; Antonsson et al. 2010). Further, growth can be positive or negative, depending on whether an individual expends less or more energy than it has stored or has obtained from food consumption (Cho et al. 1982). For fish, metabolic rate and growth are regulated by abiotic factors, such as temperature and photoperiod, and biotic factors, such as food availability (Dutta 1994). Somatic and reproductive growth, in turn, influence survival and productivity through size-selective mortality and size-based fecundity (Sogard 1997; Quinn 2005).

Pacific salmon are anadromous, semelparous, and extensive migrators; therefore, growth in body size and growth rate are influenced by freshwater and marine processes (Schindler et al. 2003). The typical Pacific salmon life cycle consists of: (1) adults spawning in a river, stream, or lake; (2) offspring hatching and utilizing freshwater environments for 0-3 years (species dependent); (3) juveniles migrating from freshwater systems to the ocean; and (4) fish maturing into sexually reproductive adults and migrating back to their natal stream to spawn and die (Dittman and Quinn 1996). Fecundity of female Pacific salmon is typically size dependent, with larger females producing more and larger eggs (Skaugstad and McCracken 1991; Quinn 2005). The fecundity of spawning females is important because it determines the potential reproductive capacity of the population each brood year (BY; Skaugstad and McCracken 1991). Although the initial size of a juvenile fish may be genetically determined and dependent on the size of their parent, somatic growth changes with each life stage and can be influenced by varying environmental and biological factors (Quinn 2005).

Maximizing growth in the freshwater environment is crucial to parr survival. Survival to adulthood and sexual maturity may be dependent on growth of juvenile fish during early life stages (Antonsson et al. 2010). This is because larger and faster-growing individuals are better able to escape size-selective survival pressures, such as predation, and have a larger gape size, which allows for the consumption of a large diversity of higher-energy prey (Sogard 1997; Thompson and Beauchamp 2014).

Large body size also aids in overwinter survival of parr. For example, Smith and Griffith (1994) found that in a cohort of Rainbow Trout *Oncorhynchus mykiss*, smaller individuals had disproportionately higher mortality than larger conspecifics and that there was a minimum length threshold (100 mm) where individuals did not survive. Fish with large body size typically have greater amassed lipid reserves that will sustain these individuals longer during low resource, high stress periods such as winter (Smith and Griffith 1994; Biro et al. 2004; Thompson and Beauchamp 2014).

Salmon migrate from freshwater to marine systems because of the enhanced growth opportunities at sea (Jonsson and Jonsson 1993; Quinn 2005). Migration timing is crucial and allows juvenile salmon to take advantage of optimal water temperatures, salinities, and food availability (Sheridan 1962). To ready themselves for seaward migrations, parr go through smoltification, which is a change in physiology and behavior to transition to the marine environment (Healey et al. 1991). Smolt physiology changes as they develop a tolerance for higher levels of salinity, lose their parr marks and turn silver in coloration, and increase their buoyancy (Saunders 1965; McCormick et al. 1998). Smolts also begin to exhibit changes in behavior, such as increased downstream orientation and schooling, reduced territoriality, and greater salinity preference (Hoar 1988; Iwata 1995; McCormick et al. 1998). For Atlantic Salmon *Salmo salar*, shifts in photoperiod and daylight trigger physiological changes, while environmental changes such as increased water temperature and depth stimulate behavioral changes (Bohlin et al. 1993; Antonsson and Gudjonsson 2002; Byrne et al. 2003, 2004). Juvenile salmon body size appears to determine when fish will migrate, with larger and faster-growing individuals migrating earlier in the season than smaller, slower-growing conspecifics because osmotic stress reduces with body size and size-dependent predation pressures (Bohlin et al. 1993, 1996; Antonsson et al. 2010). For some stocks, smolt outmigration is stimulated by environmental changes (e.g., photoperiod, water temperature, water depth), which likely correspond to optimal times of marine food availability. High smolt mortality may be due to smolts missing this optimal foraging window because migration timing that occurs too early or late (Hvidsten et al. 1998; Mortensen et al. 2000; Antonsson et al. 2010). For example, early outmigrating Pink Salmon *O. gorbuscha* from Auke Creek, Alaska, had the highest mortality rates, which were attributed to suboptimal ocean conditions (Mortensen et al. 2000). A better understanding of smolt migration timing is necessary because marine entry is a period of major mortality for salmon species.

Post-smolt growth in the ocean and its relation to survival is largely unknown for Pacific salmon. Increased growth and large body sizes may improve survival and increase individual fecundity in some stocks (Healey 1982; Ruggerone et al. 2009; Quinn 2005). Correlations between early marine growth and survival have been found for Coho Salmon *O. kisutch* and Atlantic Salmon (Holtby et al. 1990; Friedland et al. 1993). It is commonly recognized that the majority of natural marine mortality of Pacific Salmon occurs during two periods: (1) predation during the early marine period; and (2) mortality of individuals below a critical size due to their inability to meet minimum metabolic requirements of the fall and winter period of their first year at sea (Beamish and Mahnken 2001). Larger, faster-growing fish typically are released from size-selective predation pressures sooner than smaller conspecifics (Sogard 1997; Beamish and Mahnken 2001). Faster-growing individuals are also able to capture larger prey at an earlier age which can lead to improved metabolic efficiency and a further increase in growth (Quinn 2005; Ruggerone et al. 2009). In addition, energy reserve depletion is typically less rapid for larger than smaller fish and may equip larger individuals with sufficient reserves to survive periods of starvation (Sogard 1997; Beamish et al. 2004). For example, marine survival and brood-year strength of Coho Salmon stocks were observed to be partially determined by growth in the first-marine year (Beamish et al. 2004). The growth and survival of Chinook Salmon in the ocean is also likely affected by environmental conditions. Ongoing variations in climate can create a match-mismatch between salmon and their food resources, causing reduced growth and survival (Ruggerone et al. 2009).

The influence of environmental factors and growth patterns on survival, recruitment, and abundance of salmon stocks over time can be identified through retrospective growth analyses utilizing archived scale data (Friedland et al. 1993; Friedland et al. 2000; Ruggerone et al. 2007; Friedland et al. 2009; Hogan and Friedland 2010). Scales provide long-term, non-lethal, and easily collected structures to use for estimating age and growth patterns of a fish. Scales grow in a concentric fashion with visible rings that are thicker or thinner based on summer versus winter growth, respectively (Fukuwaka 1998;

Borgerson et al. 2014). Because scale growth is correlated with increases in fish length, scales can be measured and growth increments used as a proxy for fish growth (Bilton 1975; Fisher and Pearcy 2005; Friedland et al. 2009; Hogan and Friedland 2010). Scales are collected from survivors and assumed to be representative of the entire population. Retrospective growth analyses have been used to identify how patterns in growth via scale measurements relate to stock indices (e.g., freshwater and marine survival, total or in-river return) and environmental conditions (Friedland et al. 1993; Ruggerone et al. 2007; Friedland et al. 2009). For example, increased post-smolt growth was correlated to more favorable sea temperature conditions and increased survival rates of Atlantic Salmon in the North Sea (Friedland et al. 2000). Scale-growth measurements have also been used to detect the presence of growth dependency and compensatory growth or differences in growth patterns among age classes in salmon (Ruggerone et al. 2007). Overall, retrospective growth analyses utilizing long-term scale archive data have allowed researchers and managers to non-lethally detect salmon growth patterns over time and may be a useful tool for identifying how growth relates to increased variability in Pacific salmon returns.

Chinook Salmon *O. tshawytscha* are the largest of the five species of Pacific salmon, and can be distinguished from other species of Pacific salmon by their large size, black coloration on the lower jaw, and the presence of black spots on both lobes of the caudal fin (Quinn 2005). This species supports important and diverse subsistence, commercial, recreational, and personal use fisheries throughout Alaska. In Southeastern Alaska (SEAK), Chinook Salmon are primarily harvested in the commercial troll fishery and by recreational anglers, but commercial set gill net, drift gill net, and purse seine fisheries and subsistence fisheries are present as well (Der Horvanisian et al. 2011). In addition to these U.S. fisheries, Chinook Salmon are harvested by Canada in two transboundary systems, the Taku and Stikine rivers. Stock declines, increasingly variable recruitment, and historic overharvest have created social and economic hardships for communities in SEAK. Reductions in harvest as well as recovery and annual monitoring programs were initiated by the Alaska Department of Fish and Game (ADF&G) and Department of Fisheries and Oceans Canada (DFO, for transboundary stocks) in accordance with the Pacific Salmon Treaty. Through these programs which were enacted in 1985, twelve indicator tributaries throughout Alaska were selected and sampled to estimate annual escapement as part of the stock monitoring program (ADF&G Chinook Salmon Research Team 2013). Two of these indicator stocks, the Stikine and Chilkat rivers, have the second and fifth largest runs of Chinook Salmon in SEAK, respectively. Both rivers have shown long-term declines in spawner abundance and increased variability in production (McPherson et al. 2003; Der Horvanisian et al. 2011; ADF&G Chinook Salmon Research Team 2013). These systems also have long-term scale archives of adult and smolt Chinook Salmon data sets, which allow for in-depth analyses of each stock. Unlike the majority of the other indicator stocks, marine survival data for Chinook Salmon have also been collected for the Chilkat and Stikine rivers, allowing for analyses to determine if productivity declines can be attributed to declines in freshwater and/or marine survival. These data allow for the importance of freshwater and marine growth and survival on Chinook Salmon recruitment to be examined, which should lend insights into management scenarios for SEAK Chinook Salmon stocks.

Climate change and mine development are two major threats to Chinook Salmon populations in SEAK. With air temperatures predicted to increase by 1 to 5°C over the next century, thermal regimes in freshwater habitats could change and cause increased precipitation and flooding, higher freshwater and ocean temperatures, and a rise in sea level (Bryant 2009; Shanley and Albert 2014). Freshwater temperatures can influence egg development rate, egg emergence timing, freshwater growth rates, and smolt migration timing (Elliott 1988; Holtby 1988; Lawson et al. 2004). For example, increases in spring air temperatures near Coho Salmon rearing rivers in Oregon and Washington have been associated with earlier smolt migration and reduced marine survival (Lawson et al. 2004). These reductions in survival may be due to rises in sea surface temperatures, which have been associated with changes in on- and offshore prey compositions encountered by Pacific salmon during early ocean entry (Mackas et al. 2007). Populations of SEAK Chinook Salmon that are adapted to a specific environment will have to adapt to the new regimes imposed by climate change (Halupka et al. 2003; Bryant 2009). Increases in mining activity in SEAK and British Columbia, Canada, also threaten the health and longevity of these stocks. Red Chris Mine, a gold and copper mine, owned and operated by Imperial Metals (the company that also owned the failed Mount Polley Mine on the Fraser River), recently became operational on the Iskut River, a tributary of the Stikine River. Current mine explorations are also underway on the Klehini River, a tributary of the Chilkat River, near Haines, Alaska.

With the potential threats of climate change and habitat alteration, my study identified past and present factors which influence growth, survival, and recruitment of Chinook Salmon in the Chilkat and Stikine rivers. This study utilized historic scale samples and data to investigate factors that impact the survival and recruitment strength of these regionally important Chinook Salmon stocks throughout their life cycle in freshwater and marine environments. Chapter one examined how annual freshwater and marine growth influenced BY recruitment success of Chinook Salmon from the Chilkat and Stikine rivers. The second chapter characterized the downstream smolt outmigration of Chinook Salmon from the Chilkat River and identified the impacts of environmental and biological factors on outmigration timing. Finally, chapter three examined the influence of environmental and biological factors on overwinter survival, smolt production, and marine survival of Chinook Salmon from the Chilkat and Stikine Rivers. This research not only provided insights into factors influencing the recruitment variability of these two Chinook Salmon stocks, but also increased our understanding of the freshwater and marine conditions that influence growth and survival in Pacific Salmon.

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Chapter 1: Evaluation of growth and survival on recruitment of Chinook Salmon in Southeastern Alaska rivers[1]

Abstract

Increased variability in recruitment success of Chinook Salmon *Oncorhynchus tshawytscha* has caused social and economic hardships throughout Alaska. Pre- and post-smolt growth may influence the survival and productivity of Chinook Salmon through size-mediated mortality; however, these relationships remain unclear. This study used archived scale data and conducted a retrospective growth analysis to identify the importance of annual growth in determining brood-year (BY) survival and recruitment, detect the presence of growth dependency between growth zones, and examine growth differences among age classes for Chinook Salmon in the Chilkat (BYs 1985 – 2007) and Stikine (BYs 1991 – 1992 and 1995 – 2007) rivers. Increased first-year marine growth was correlated with higher BY total return (R^2 = 0.2) and productivity (R^2 = 0.52) for Chinook Salmon from the Chilkat River and higher BY total return (R^2 = 0.71) and productivity (R^2 = 0.31) for Chinook Salmon from the Stikine River. Marine survival of Chinook Salmon from the Stikine River was significantly correlated with both freshwater and first-year marine growth and the model explained 85% of the variability in marine survival. Growth during the first marine year was significantly related to freshwater growth (r = 0.12) for Chilkat River Chinook Salmon. In the Stikine River, growth during the second year at sea was weakly but significantly related to growth during the first year at sea (r = 0.19). Growth of age-1.3 Chinook Salmon began to exceed that of age-1.4 fish during the freshwater rearing phase in both the Chilkat and Stikine rivers and growth continued to be higher for age-1.3 fish during each subsequent growth zone. These results indicate that increases in the variability of recruitment success and reductions in returns for Chinook Salmon in SEAK may be due to growth conditions during ocean entry and the first year at sea.

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Introduction

Growth is a major factor effecting the survival and productivity of Pacific salmon *Oncorhynchus* spp. (Healey 1982; Quinn 2005; Ruggerone et al. 2009; Antonsson et al. 2010). When the energy expenditure of an individual is less than the energy content of consumed food, growth occurs (Cho et al. 1982). For diadromous fishes, growth in body size and growth rate are influenced by freshwater and marine processes. All Pacific salmon are anadromous, semelparous, and extensive migrators; therefore, they spend crucial periods of their life history in both freshwater and marine environments (Schindler et al. 2003). The critical size, critical period hypothesis states that brood-year (BY) strength of Pacific Salmon is determined during two periods: (1) predation during the early marine period; and (2) mortality of individuals below a critical size due to their inability to meet minimum metabolic requirements in the fall and winter of their first year at sea (Beamish and Mahnken 2001). Greater growth and size during the freshwater rearing phase has been linked to higher survival to adulthood and sexual maturity because greater fish body length reduces predation mortality and prey-size limitations during the early marine entry period (Koenings et al. 1993; Antonsson et al. 2010; S. Berkman, UAF, unpublished data). Correlations between early marine growth rate and survival have also been observed in other salmon species, including Chinook Salmon *O. tshawytscha*, Coho Salmon *O. kisutch,* and Atlantic Salmon *Salmo salar* (Holtby et al. 1990; Friedland et al. 1993; Murphy et al. 2013). Longer, faster-growing individuals are able to capture larger prey at an earlier age, which can lead to improved metabolic efficiency and a further increase in growth (Quinn 2005; Ruggerone et al. 2009). In addition, larger individuals deplete their energy reserves less rapidly than smaller conspecifics and are better equipped to survive periods of starvation during their first fall and winter at sea (Sogard 1997; Beamish et al. 2004). Overall, growth and larger body sizes attained in freshwater may reduce predation mortality during the early marine period while increases in growth rate and condition during the first summer at sea may minimize mortality caused by metabolic deficiencies during the first winter at sea (Beamish and Mahnken 2001).

Because of size- and growth-based survival advantages present during the freshwater and early marine rearing period, reductions in growth and body size may lead to lower BY strength (Sogard 1997; Beamish and Mahnken 2001; Beamish et al. 2004).

Environmental factors can affect both somatic and reproductive growth through variations in water temperature and food availability (Wootton 1998; Quinn 2005). Because fish are poikilotherms, external water temperature plays one of the most important roles in regulating metabolic rate and growth (Cho et al. 1982). Fish typically have a specific optimal temperature or range of temperatures for growth, which is species and region specific, where metabolic rate is most efficient and growth is maximized (Wootton 1998). Food availability is also important as it supplies the energy needed to maintain life processes, growth, and reproduction (Cho et al. 1982; Wootton 1998). Due to the importance of temperature to growth, variations in oceanic conditions and productivity can impact survival and BY recruitment strength of Pacific salmon stocks as well (Friedland et al. 2000; Mueter et al. 2005). For example, sea surface temperatures (SSTs) in Auke Bay, Alaska, were positively related to early marine growth of Pink Salmon *O. gorbuscha* which, in turn, was positively related to survival to adulthood (Mortensen et al. 2000). Similar patterns have also been detected for Atlantic Salmon in the North Sea, where higher SSTs resulted in higher first-year marine growth and return rates (Friedland et al. 2000). Mueter et al. (2005) observed that SSTs in nearshore during the early marine period influenced survival rates of Pink Salmon, Chum Salmon *O. keta*, and Sockeye Salmon *O. nerka*. Ongoing variations in climate can also cause changes in on- and offshore prey compositions encountered by Pacific salmon during early ocean entry (Mackas et al. 2007). These climate-induced changes can lead to matches and mismatches between marine-entry timing of salmon relative to their food resources, which can enhance or limit BY growth and survival during this critical early marine period (Lawson et al. 2004; Ruggerone et al. 2009; Vega et al. 2017). Increases in SSTs and corresponding changes in freshwater, estuarine, and marine dynamics have been associated with increased mismatch situations (Gargett 1997; Lawson et al. 2004). It is likely that Pacific salmon stocks will need to adapt to new regimes imposed by climate change, and it is imperative for managers to understand the current interactions between salmon growth, survival, and the climate to successfully manage stocks (Halupka et al. 2003; Bryant 2009). These stock- and species-specific relationships can be identified using archived scale collections from spawning salmon.

Retrospective growth analyses utilizing archived scale data can be used to link environmental factors and growth patterns to trends in survival, recruitment, and abundance of salmon populations (Friedland et al. 1993; Friedland et al. 2000; Ruggerone et al. 2007; Friedland et al. 2009; Hogan and Friedland 2010). Scales provide a long-term, non-lethal, and easily collected structure to use for estimating age and growth patterns of fish. Scales grow in a concentric fashion, which are visible as circular rings called circuli. As fish grow, more circuli are deposited on the scale (Fukuwaka 1998). During the summer when growth conditions are typically greater, circuli are thicker and more widely spaced than they are in the winter when conditions are not as favorable and growth slows (Fukuwaka 1998; Borgerson et al. 2014). Scale circuli increment width measurements are correlated with growth in fish length and can be used as a proxy of fish growth through its lifetime (Bilton 1975; Fisher and Pearcy 2005; Friedland et al. 2009; Hogan and Friedland 2010; Walker and Sutton 2016). Growth analyses have been used to increase the understanding of a diverse array of information about salmon species including how growth influences important recruitment benchmarks such as total return and marine survival, presence of compensatory growth or growth dependency, and differences in growth patterns among age classes (Ruggerone et al. 2007; Friedland et al. 2009). For example, scale growth patterns have been used to examine interrelationships among growth, climate, and survival, where enhancements in growth from favorable SSTs resulted in increased survival of Atlantic Salmon (Friedland et al. 2000). Ruggerone et al. (2007) found that growth of age-1.3 Chinook Salmon from the Yukon and Kuskokwim rivers began to exceed the growth of age-1.4 fish during freshwater residence and the first year at sea, indicating that fish that mature earlier tend to grow faster throughout their life. However, a limitation of using scale measurements as a proxy for fish growth is that scales only relate to fish length. Greater fish length can influence survival by improving predator avoidance mechanisms (swimming ability) and reducing predator gape-size limitations. In contrast, greater weight and body condition, which would not be reflected by scale growth patterns, increases tolerance to adverse environmental conditions and suboptimal prey availability (Sogard 1997; Quinn 2005; Ruggerone et al. 2009). As a result, the sole use of scales to better understand fish growth may not completely characterize growth dynamics. Further, scale samples are primarily collected only from surviving adults and, therefore, may not be representative of the entire stock because fish that suffer mortality are not included in the analyses (Friedland et al. 1993). Regardless of these caveats, the use of long-term scale archive data has been effective for identifying growth patterns and evaluating factors that influence survival and recruitment of Pacific salmon populations and can be utilized to better understand regional salmon stocks.

Chinook Salmon support important and diverse subsistence, commercial, personal use, and recreational fisheries throughout the state. Stock declines, increasingly variable recruitment, and historic overharvest have created social and economic hardships for communities in Southeastern Alaska (SEAK; ADF&G Chinook Salmon Research Team 2013). Because of these stock trends and increased variability in climate patterns, it is imperative to better understand Chinook Salmon growth and how it has related to temporal trends survival and BY recruitment. Annual monitoring programs initiated by the Alaska Department of Fish and Game (ADF&G) and Department of Fisheries and Oceans Canada (DFO, for transboundary stocks) in accordance with the Pacific Salmon Treaty allow for a long-term analysis on how growth influences the survival and recruitment of Chinook Salmon in SEAK (ADF&G Chinook Salmon Research Team 2013). The goal of this study was to conduct a retrospective growth analysis using archived scale data to identify the importance of annual growth in determining survival and recruitment of two regionally important SEAK stocks of Chinook Salmon. Specific objectives include the following: 1) identify how annual freshwater and marine growth influenced BY recruitment success of Chinook Salmon; 2) determine if growth dependency or compensatory growth was present in Chinook Salmon; and 3) examine growth differences among age classes. By providing a more thorough understanding of Chinook Salmon growth patterns and how freshwater and marine growth influenced BY recruitment strength of geographically distinct salmon stocks, managers will be able to develop more accurate and reliable forecasts for making management decisions on Chinook Salmon in SEAK rivers.

Methods

Study Sites

The Chilkat and Stikine rivers were selected for this study because they support important regional Chinook Salmon stocks, are geographically distinct, and long-term data exists for both systems. Differences in the marine rearing locations of these two stocks allowed for a more region-wide perspective on the relationships between growth, survival, and recruitment for Chinook Salmon throughout SEAK. In addition, impending threats, like climate change and increased mining activity in British Columbia and SEAK, may expose these stocks to further declines.

Chilkat River

The Chilkat River supports the fifth largest stock of Chinook Salmon in SEAK, with a spawning run size of about 4,000 large (> 660 mm mid-eye fork length [MEF]) fish annually (McPherson et al. 2003; ADF&G Chinook Salmon Research Team 2013). The river is a moderately sized, glacially fed system that originates at Chilkat Glacier in British Columbia, Canada, and drains into the Lynn Canal near Haines, Alaska (Figure 1.1; ADF&G Chinook Salmon Research Team 2013; Chapell and Elliott 2013). Harvest of Chilkat River Chinook Salmon is conducted through commercial troll, drift gill net, and purse seine fisheries, recreational fisheries, and local subsistence fisheries, with recent harvest rates around 16% of the total run annually (ADF&G Chinook Salmon Research Team 2013; Elliott and Power 2015). Chilkat River Chinook Salmon have a stream-type life history where the majority of juveniles reside in freshwater for one year before migrating downstream as smolts. Based on Coded Wire Tag (CWT) recovery data, Chinook Salmon from this stock rear primarily in the northern inside waters of SEAK and Northern British Columbia (ADF&G Chinook Salmon Research Team 2013; Chapell and Elliott 2013).

Chinook Salmon abundance data in the Chilkat River was acquired through a juvenile CWT and an adult mark-recapture study, while harvest data was obtained through subsistence permits and a creel survey (Chapell and Elliott 2015). The mark-recapture study began in 1991 in order to estimate Chinook

Salmon inriver abundance, escapement, and age-sex-length compositions. The juvenile Chinook Salmon CWT survey was initiated in 2000 to estimate parr and smolt abundance, smolt emigration, and marine harvest of the Chilkat River stock (Chapell 2013).

Stikine River

The Stikine River supports the second largest stock of Chinook Salmon in SEAK, with a spawning run size of approximately 22,000 large (> 660 MEF length) fish annually (ADF&G Chinook Salmon Research Team 2013). The river is a transboundary system originating in British Columbia that drains into the Gulf of Alaska near Wrangell, Alaska (Figure 1.1; Jaecks et al. 2013). Since 2005, harvest rates have been roughly 50% of the stock, with most harvests occurring by U.S. commercial gill net and recreational fisheries near the mouth of the river and Canadian gill net and aboriginal fisheries in-river (Bernard et al. 2000; ADF&G Chinook Salmon Research Team 2013). More recently, the pre-season run forecast, which must exceed 28,100 fish to allow direct commercial fisheries, has not been sufficient to allow any commercial harvest (Jaecks et al. 2015). Stikine River Chinook Salmon have stream-type life history and, similar to the Chilkat River stock, spend one year in freshwater before migrating to the sea. Based on CWT recoveries, these fish mostly rear in the Bering Sea and Gulf of Alaska (ADF&G Chinook Salmon Research Team 2013).

Given that the Stikine River is a transboundary river, monitoring of this Chinook Salmon stock is conducted by the ADF&G, DFO, and Tahltan First Nation (TFN). Chinook Salmon abundance data were acquired through adult mark-recapture and a juvenile CWT studies, similar to those conducted in the Chilkat River (Jaecks et al. 2015). The monitoring of Chinook Salmon escapement in the Stikine River began in 1981, with counting spawners at Little Tahltan River and Andrew Creek. With the need for more accurate and reliable escapement estimates, a mark-recapture program was established in 1996 and remains in place. Most escapement and abundance estimates reports only include large (> 660-mm MEF) Chinook Salmon because fish below this length are typically young (i.e., 1.1, 1.2) jacks (ADF&G Chinook Salmon Research Team 2013; Jaecks et al 2015). The juvenile CWT study was initiated in 2005 to estimate the number of smolts emigrating from the Stikine River and the harvest rate of Stikine River adult Chinook Salmon in commercial and recreational fisheries (ADF&G Chinook Salmon Research Team 2013).

Recruitment benchmarks

Total return, productivity, and marine survival of Chinook Salmon in the Chilkat and Stikine rivers were used as recruitment benchmarks in this study. All estimates were obtained from ADF&G and were made through their respective mark-recapture and CWT studies. Total return was the sum of in-river spawner abundance of age-1.2 to 1.5 fish and the marine and in-river harvest for each BY. Brood-year productivity, or recruits per spawner, was calculated using the total return from a given BY divided by the number of spawners (as determined via escapement estimates) that produced that cohort. Marine survival was calculated by dividing the estimated BY total return by the estimated BY smolt abundance.

Scale samples and scale reading

To construct a scale-based time series of Chinook Salmon growth, scale samples of female age-1.3 and 1.4 Chinook Salmon from both the Chilkat and Stikine rivers were collected during the ADF&G two-event mark-recapture project. Freshwater and marine growth patterns were analyzed using the scales from 50 different fish (25 individuals per age-class) from the Chilkat River (BYs 1985 – 2007) and the Stikine River (BYs 1991 – 1992 and 1995 – 2007). The scale sampling procedure included the removal of five scales from the "preferred area", which is located on the left side of each sampled fish in an area 2-4 scale rows above the lateral line and between the dorsal fin and anal fin (Hagen et al. 2001). Scales were placed on gum cards to make acetate impressions, which were later scanned into a computer for aging and measurement (Hagen et al. 2001). Only female Chinook Salmon scales were analyzed because female body size is a better representation of annual production capacity and is directly correlated with fecundity (Skaugstad and McCracken 1991; Quinn 2005). Females also have fewer age classes that return at reproductive maturity (primarily ages 1.3 and 1.4) than males (ages 1.1-1.4), which reduced the number of age classes and scales required for analysis. The scales used in this research were collected from adults that survived to sexual maturity and therefore, associated biases were considered in analyses and interpretation of results.

The scale analysis procedure took place at the ADF&G Mark, Tag, and Age Laboratory (MTAL) in Juneau, Alaska, where scales were processed as outlined in Hagen et al. (2001). Gum cards containing scale samples were used to make acetate slides, which were digitalized with a Screenscan ® Microfiche Scanner. Digitalized scale images were loaded into ImagePro Plus (Version 7.0, Media Cybernetics Inc., Rockville, Maryland) and measured using the Otolith Analysis macro written by the ADF&G MTAL following established measuring protocol. Measuring scales first required the identification of annual freshwater and marine growth zones, as well as the individual circuli in each growth zone (Figure 1.2). There was a noticeable difference between the circuli deposited during freshwater and marine growth phases. Freshwater growth (pre-smolt) circuli were typically thin, light in color, and close together, while marine growth (post-smolt) circuli were thicker, darker in color, and more widely spaced (Borgerson et al. 2014). Each year of growth was characterized by an area of tightly spaced and wider spaced circuli, representing slower winter growth and faster summer growth, respectively (Figure 1.2; Ruggerone et al. 2009). Growth zones were classified in Image Pro Plus using methods detailed in Hagen et al. (2001). Quality-control reviews of the scales were conducted throughout the measuring process to ensure reader consistency and accuracy. Scale metadata, such as fish length, collection date, collection location, and sampling gear type, were included in the final dataset for each study river.

The scale samples used in this study from Chinook Salmon in the Stikine River were collected using gill nets of one mesh size during event one of the mark-recapture study and were combined into a single sample. Scale samples from the Chilkat River were collected during events one and two of the mark-recapture study through use of dip nets, drift gill nets with two mesh sizes, fish wheels, hand picking (carcass surveys), set gill net, snagging, and a weir. Analysis of variance (ANOVA) tests were conducted on Chilkat River scale samples to determine if scale growth zone measurements differed among gear types. Significant differences in growth zone measurements were detected in fish that were collected by some gear types that were used only in early or later sampling years (i.e., weirs, snagging, set gill net); therefore, those samples were removed (N = 59) and all other scale samples were pooled for analysis.

Growth and recruitment benchmarks

Simple linear regression was used to identify trends in growth zones over time. Multiple and simple linear regression were used to determine relationships between annual Chinook Salmon growth zones and log-transformed BY recruitment benchmarks (i.e., total return [Chilkat River: N = 21, Stikine River: N = 15], productivity [(Chilkat River: N = 17, Stikine River: N = 15], and marine survival [Chilkat and Stikine rivers: N = 10]). Annual growth zones were the measured length (µm) of that zone and were represented as FW1 for freshwater growth and SW1, SW2, SW3, and SW4 for each year of marine growth. The two rivers were modeled separately because of their geographically distinct freshwater and marine rearing locations. Differences in the BY abundance of age-1.3 and 1.4 fish were addressed by computing weighted means for each annual growth zone using BY age-class abundance estimates as weights. Log-transformed recruitment benchmarks by BY (dependent variable) were modeled as a function of these weighted mean growth zones (independent variables). Because scale sample sizes varied among BYs, each BY in the multiple and simple linear regression models was weighted by the number of scale samples using weighted-least-squares regression. Full models were fitted for log-transformed total return and productivity as a function of all growth zones, and top models were selected using a stepwise approach based on the lowest Akaike Information Criterion (AIC). Diagnostics were conducted on the top models to ensure that the assumptions of linear regression were met, and quadratic terms were included in models if diagnostics suggested a pattern in residuals. Due to the small number of BYs with marine survival estimates, only those growth zones that were significantly correlated to BY total return and productivity were included in models of marine survival. Freshwater growth was included in the model of Stikine River Chinook Salmon marine survival, regardless of the significance in other models, because previous research has indicated a significant relationship between smolt length and marine survival of this stock (S. Berkman, UAF, unpublished data). Statistical significance was assessed at an $\alpha \leq 0.05$, and all analyses were conducted using R 3.2.2 (R Core Team 2014).

Growth dependence and differences in life stage growth

Growth dependency, i.e., the relationship between annual growth and growth that occurred during the subsequent year (e.g., FW1 versus SW1, SW1 versus SW2, etc.), was examined using simple linear regression. To determine at which life stage growth of age-1.3 fish began to exceed that of age-1.4 fish, two-sample t-tests were used to compare each annual growth zone between age classes.

Results

The weighted annual growth of Chinook Salmon from the Chilkat and Stikine rivers was highest during the first year of marine residency and declined with each additional year at sea (Table 1.1). Weighted BY growth during the fourth year at sea (SW4) significantly declined over the time series for the Chilkat River (Table 1.1; BY1987 - 2007). No other significant temporal trends in weighted annual BY growth were detected in either river system (Table 1.1).

Growth and recruitment benchmarks

For Chilkat River Chinook Salmon, growth during the first year at sea (SW1) was the only growth zone significantly related to the BY total return and productivity (Table 1.2). First-year marine growth accounted for 20% and 52% of the variability in BY total return and productivity, respectively. Growth during the first year of marine residency was not significantly related to marine survival and accounted for none of the variation in marine survival (Table 1.2).

In the Stikine River, first-year marine growth was significantly correlated with log-transformed BY total return and explained 67% of the variability (Table 1.2). The relationship was best represented as quadratic and suggested an increase in BY total return when SW1 growth was high (Figure 1.3). First-year marine growth was positively and significantly correlated with log-transformed BY productivity and explained 33% of the variability (Table 1.2). Both FW1 and SW1 growth were significantly related to marine survival of Chinook Salmon in the Stikine River (Figure 1.3; Table 1.2), and explained 81% of the variation in marine survival.

Growth dependence and differences in life stage growth

Growth during the first marine year was positively and significantly related to growth during the freshwater life stage of age-1.3 and 1.4 Chinook Salmon in the Chilkat River (Figure 1.4; $r = 0.12$, $P = <0.001$). For Stikine River Chinook Salmon, positive growth dependency was present between SW2 and SW1 growth zones ($r = 0.19$, $P < 0.0001$). Growth dependency was not detected between any other growth zones.

Growth of age-1.3 Chinook salmon from both the Chilkat and Stikine rivers exceeded that of age-1.4 fish during the freshwater life stage. All age-1.3 growth zones were significantly different and larger than age-1.4 growth (Table 1.3). Growth was between 3-11% higher for age-1.3 salmon from the Chilkat River and 6-16% higher for age 1.3 salmon from the Stikine River. The largest difference in growth occurred during the second year at sea for the Chilkat and Stikine rivers where age-1.3 fish grew on average 11% and 16% more than age-1.4 fish, respectively.

Discussion

Results from the current study suggest unique and dynamic relationships between growth, survival, and recruitment of Chinook Salmon in SEAK. Annual growth during the fourth marine year declined over time in the Chilkat River, while there were no significant temporal trends in the annual growth patterns in the Stikine River. Graham (2016) also noted the absence of temporal patterns in growth for Chinook

Salmon in the Unuk and Taku rivers, which are located nearby in SEAK. A multi-decadal growth analysis conducted on Chinook Salmon from the Yukon and Kuskokwin rivers, Alaska, showed oscillating patterns in growth, which was correlated to oceanic-regime shifts (Ruggerone et al. 2007). Similar oscillating patterns have been detected in the post-smolt growth of Atlantic Salmon from the Miramichi River, Canada, where marine growth increased over time (Friedland et al. 2009). Previous research on the interactions of climate, food availability, and salmon growth found that larger fish have lower optimal temperatures for growth and that these thermal thresholds can further decline when food resources are limited (Beauchamp 2009). The decline in growth of age-1.4 Chinook Salmon during the final year at sea for fish from the Chilkat River, but not the Stikine River, may indicate that sea temperatures and food resources have become less optimal for growth over time in nearshore areas. In contrast, Bigler et al. (1996) detected a reduction in body size of nine Chinook Salmon stocks throughout their Alaskan range and suggested that these declines were caused by increases in Pacific salmon abundance through improved management and stocking that led to a reduction in the available offshore marine food resources which, in turn, limited growth.

Growth and recruitment success

The retrospective growth analyses conducted in the current study indicated that annual growth was related to recruitment success of Chinook Salmon from the Chilkat and Stikine rivers. In particular, first-year marine growth was positively correlated to recruitment indices for both stocks. The relationships between SW1 growth and the recruitment benchmarks observed in these stocks suggests that the sample of survivors used in these analyses was representative of the Chinook Salmon populations in the Stikine and Chilkat rivers (Friedland et al. 1993; McCarthy et al. 2008). These results are consistent with previous studies and demonstrate the importance of first-year marine growth in determining BY recruitment strength of Pacific salmon stocks (Holtby et al. 1990; Beamish and Mahnken 2001; Tomaro et al. 2012). The critical size, critical period hypothesis suggests that reaching a certain minimum size during the first summer at sea is a critical determinant of stock BY recruitment strength (Beamish and Mahnken 2001).

Greater first-year marine growth was correlated to higher BY total return and productivity for Chinook Salmon from the Chilkat River and higher BY total return, production, and marine survival for Chinook Salmon from the Stikine River. Increased growth during the first year at sea can reduce size-selective mortality by releasing fish from forage-based gape limitations and predation pressures (Koenings et al. 1993; Sogard 1997; Mortensen et al. 2000). Larger fish are also better equipped to withstand periods of starvation as they deplete energy reserves less rapidly on a per unit body mass basis than smaller conspecifics (Beamish et al. 2004). For Stikine River Chinook Salmon, the weak relationships between BY total return and productivity and SW1 growth below 1.33 μm may indicate that greater early marine growth only positively influences total return and productivity above a certain threshold. The results in the current study suggest that the recent increases in variation and declines in total return and productivity observed in these two Chinook Salmon stocks are, in part, a result of growth rates and conditions during the first year at sea.

Growth in freshwater was positively related to marine survival of Chinook Salmon from the Stikine River. Size-based marine survival advantages for larger smolts upon marine entry have been observed for Chinook, Coho, Pink, Sockeye, and Atlantic Salmon (Holtby et al. 1990; Koenings et al. 1993; Mortensen et al. 2000; Antonsson et al. 2010; Murphy et al. 2013). The increase in survival is likely a result of reduced predation through increased escapeability mechanisms and faster growth rates for larger smolts (Koenings et al. 1993; Sogard 1997; Beamish and Mahnken 2001). Larger smolts have fewer gape limitations and can consume larger, more energy-rich prey items than smaller conspecifics, which further enhances growth opportunities (Quinn 2005). The absence of a significant relationship between freshwater growth and the survival and recruitment of Chinook Salmon from the Chilkat River may indicate that growth during the first-marine year is more important than size at ocean entry in determining BY recruitment success. Hogan and Friedland (2010) similarly detected no correlations between freshwater growth and recruitment in Atlantic Salmon from rivers in Maine. The authors suggested that the absence of a growth-recruitment relationship may have been a result of greater size-independent predation by more abundant predators and reduced predatory avoidance behaviors caused by high levels of osmotic stress in coastal nursery areas. Tomaro et al. (2012) detected that marine growth rates within the first 30 days at sea, and not size at ocean entry, were positively related to the adult returns of Chinook Salmon from the Columbia River, Washington. These results and the results from the current study indicate that growth rate during the first-marine year and the time it takes an individual to attain a size large enough to escape predation pressures was more important than size at ocean entry in determining BY recruitment success in nearshore nursery areas. In other salmon stocks, large smolt body size only influenced survival and recruitment during years of poor survival (Holtby et al. 1990; Woodson et al 2013; Graham 2016). For example, Chinook Salmon smolt body size from the Unuk River, Alaska, was only positively and significantly related to marine survival in years when marine survival was below average (Graham 2016). The author suggested that favorable early marine conditions may have allowed for increased growth and reduced size-selective mortality in smaller individuals, which concealed any survival advantages of larger smolts. Similarly, Holtby et al. (1990) observed survival advantages for larger smolts when survival was low; however, these authors noted that growth opportunities during the early marine period would be a better determinant of BY recruitment.

Climactic variation during the early life stages of salmonids following ocean entry is considered a primary determinant of growth and marine survival (Mueter et al. 2005; Hogan and Friedland 2010). Sea surface temperatures in marine rearing zones occupied by salmon smolts can influence the efficiency of metabolic and growth rates, while spring transitions in temperature change, upwelling, and light intensity influence biological production blooms that support growth of salmon from the bottom up (Gargett 1997; Wootton 1998; Tomaro et al. 2012). The dynamics of these relationships are complex and vary based on regional oceanic conditions. For example, Mueter et al (2002) detected that warmer coastal SSTs were related to higher marine survival of Pacific salmon stocks in Alaska relative to stocks further south. The authors also noted that SST was likely a proxy for other oceanic mechanisms that influence salmon survival such as upwelling and downwelling; these factors, in conjunction with SST, influence regional predator and prey abundance and distribution. Marine survival of Pink Salmon in Auke Creek, Alaska, has been shown to be lowest for early outmigrating smolts that entered the ocean when both SST and prey densities were low (Mortensen et al. 2000). Juvenile body size of Chinook Salmon during the early marine period has also been linked to the community structure of copepods, which likely influenced the fish and decapods Chinook Salmon prey upon in the ocean (Tomaro et al. 2012). Although the current study did not investigate how marine conditions influenced the growth of Chinook Salmon from the Chilkat and Stikine rivers, the large percentage of unexplained variation in recruitment, productivity, and marine survival of these stocks is likely related to changes in these conditions and should be the focus of future research.

Growth dependence and differences in life stage growth

In the current study, differences were observed in the growth patterns of Chinook Salmon from the Chilkat and Stikine rivers. Growth dependency was observed between SW1 and FW1 growth in fish from the Chilkat River and between SW2 and SW1 growth in fish from the Stikine River. Positive relationships between growth and growth in subsequent years have been observed for other Chinook Salmon stocks in Alaska (Ruggerone et al. 2009; Leon 2013; Graham 2016). Positive interactions between growth zones may be a result of greater foraging opportunities for larger individuals that are able to shift to piscivorous diets earlier than smaller conspecifics (Healey 1991; Ruggerone et al. 2009). Although freshwater growth was not correlated to recruitment of Chinook Salmon from the Chilkat River, the relationship between first-year marine and freshwater growth suggests some importance in freshwater rearing conditions to recruitment success of this stock. Higher freshwater growth may reduce the amount of time an individual is vulnerable to predators or restricted by gape-size during early marine residency (Duffy and Beauchamp 2011). In addition, the absence of a relationship between pre- and post-smolt growth for Chinook Salmon from the Stikine River suggests that freshwater growth opportunities do not incur marine growth opportunities in all individuals. Friedland et al. (2006) also found no evidence for pre- and post-smolt growth dependency. First-year marine growth may be more dependent on growth conditions like SST and prey base than previous growth in freshwater environments.

For most Pacific salmon stocks, individuals with the fastest growth rates are the first to mature, while fish with slower growth rates mature later and at larger body sizes (Quinn 2005). In the current study, growth of age-1.3 Chinook Salmon began to exceed that of age-1.4 fish during the freshwater rearing phase in both the Chilkat and Stikine rivers and growth continued to be higher for age-1.3 fish during each subsequent growth zone. Similar results were detected for Chinook Salmon from the Yukon and Kuskokwim rivers in Alaska (Ruggerone et al. 2007). Because female body size is a significant factor contributing to reproductive success of salmon stocks, changes in the survivorship of age classes can influence BY recruitment (Quinn 2005). In addition, increased age-class diversity has been shown to reduce variability in recruitment because it reduces the likelihood that all individuals in a BY will experience suboptimal growth and survival conditions (Schindler et al. 2010). Increases in the ratio of sexually mature age-1.3 to 1.4 Chinook Salmon returning to the Chilkat and Stikine rivers has been observed over the time series of this study (B. Elliott and T, Jaecks, ADF&G, unpublished data). Lewis et al. (2015) observed similar shifts in age-class abundance in 10 Chinook Salmon stocks in Alaska and noted that these shifts were due to size-selective fisheries, climate-induced growth pattern shifts, and reduced forage opportunities from density-dependent interactions. In Pink Salmon, parental body size negatively influenced stock productivity and both egg size and fecundity were positively correlated with offspring body size and subsequent survival (Wertheimer et al. 2004). The increase in mature age-1.3 fish and the decline in larger age-1.4 fish on the spawning grounds likely affected the overall reproductive success and productivity of these stocks because smaller females produce smaller and fewer eggs and offspring (Skaugstad and McCracken 1991; Quinn 2005; Lewis et al. 2015).

For the Chilkat and Stikine rivers, annual growth explained some of the variation in the BY recruitment benchmarks of Chinook Salmon. For both stocks, higher growth during the first year at sea was correlated to increased BY recruitment, productivity, and/or marine survival. These results corroborate previous research on Pacific salmon on the importance of growth during early marine residence on recruitment and survival (Beamish et al. 2001; Mortensen et al. 2000; Murphy et al. 2013). They also suggest the presence of long-term selective marine mortality that favored fish that had the fastest growth rates. Faster-growing fish typically mature at earlier ages and may be manifested in skewed age-class proportions observed for these two stocks. The production of smaller offspring by smaller and younger individuals may have further reduced size in both stocks. Changes in both freshwater and marine conditions caused by climate change and past size-selective fishing pressure have likely contributed to the reduced diversity and resilience of these stocks (Ricker 1980; Friedland et al. 2009; Schindler et al. 2010). As climate change progresses, seasonal markers, which trigger salmon migrations, will shift and further influence the survival and recruitment of these important Chinook Salmon stocks. Future research should focus on obtaining a better understanding of how climactic shifts over time and seasonally relate to marine migration timing, growth, survival, and BY recruitment.

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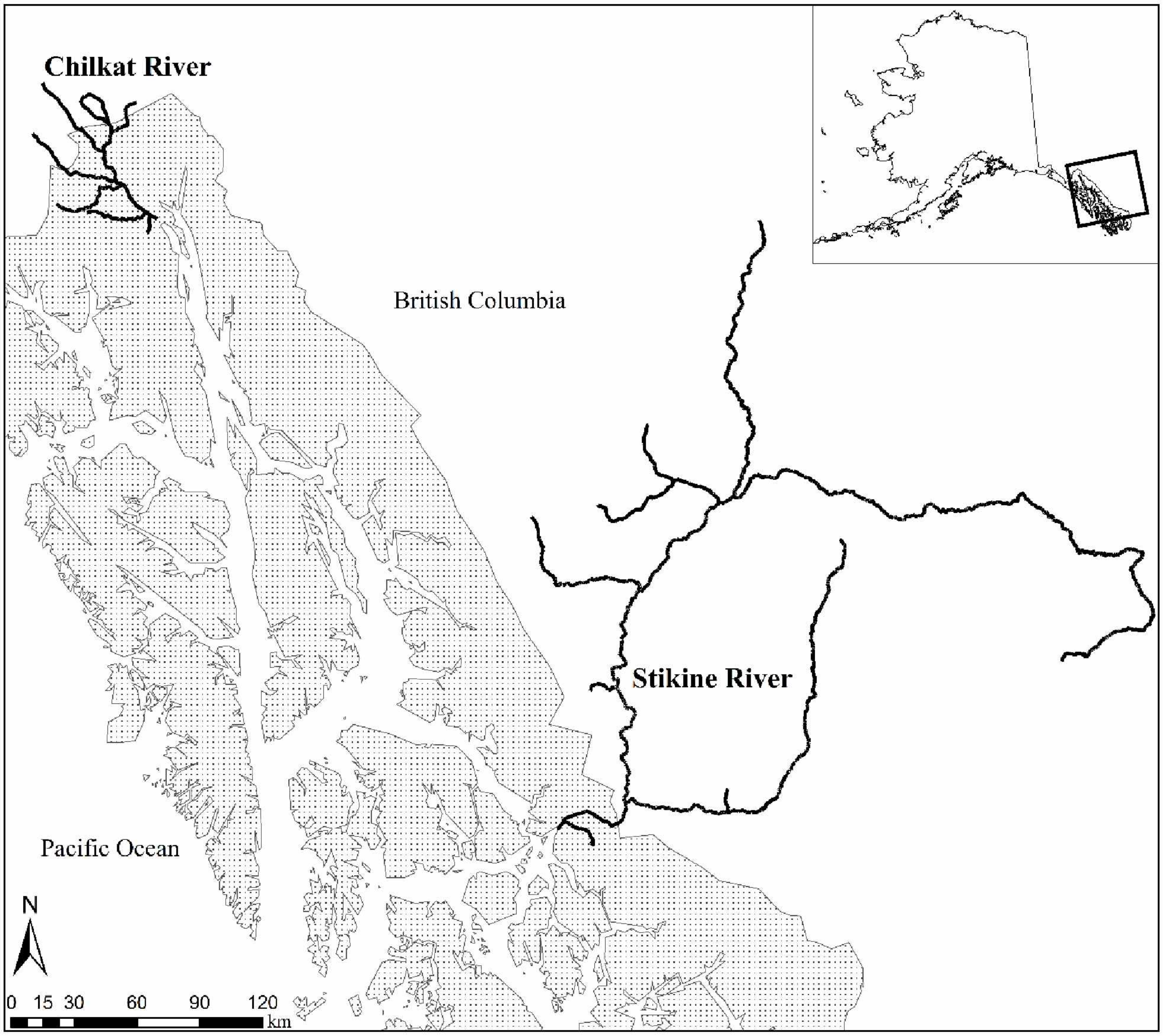

Figure 1.1. Location of the Chilkat and Stikine rivers in Alaska and British Columbia.

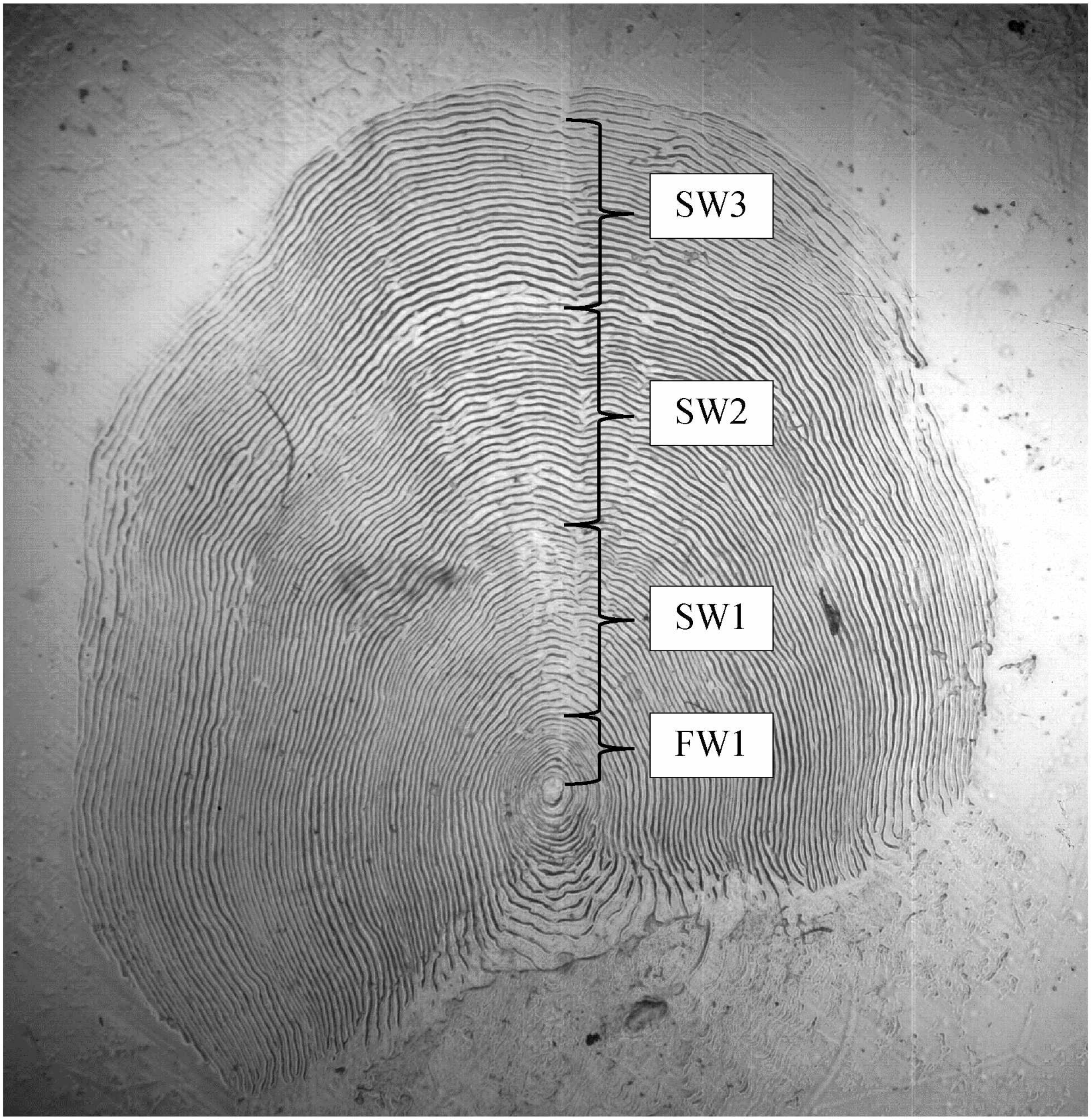

Figure 1.2. Digitalized scale image from an age-1.3 Chinook Salmon from the Chilkat River displaying freshwater growth (FW1) and the first (SW1), second (SW2), and third (SW3) year marine growth.

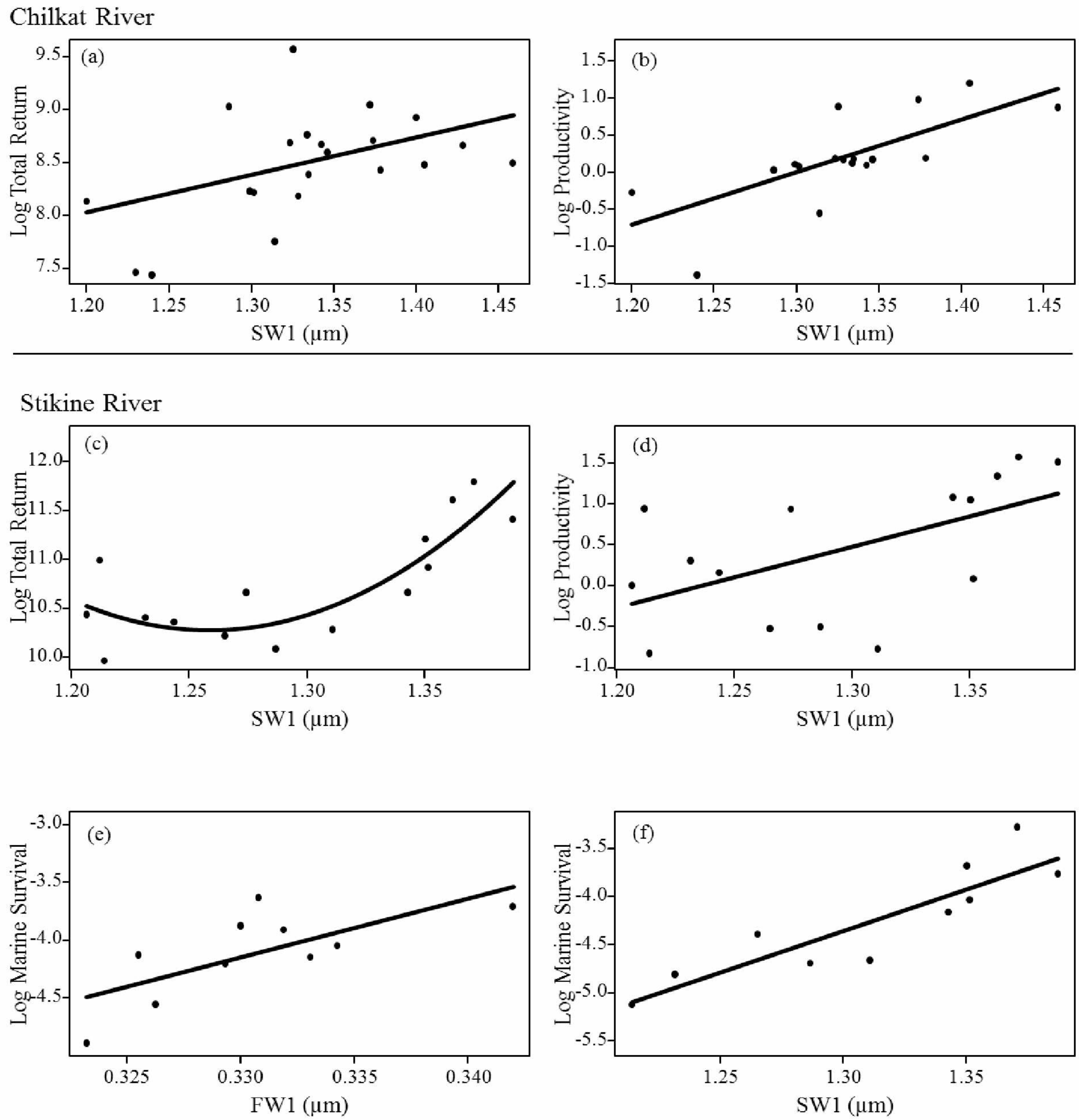

Figure 1.3. Scatter plots showing statistically significant relationships between Chinook Salmon (a) first-year marine growth and total return, (b) first-year marine growth and productivity for the Chilkat River and (c) first-year marine growth and total return, (d) first-year marine growth and productivity, (e) freshwater growth and marine survival, and (f) first-year marine growth and marine survival for the Stikine River. Solid lines represent (a) quadratic and (b, c, d, e) linear relationships from regression models.

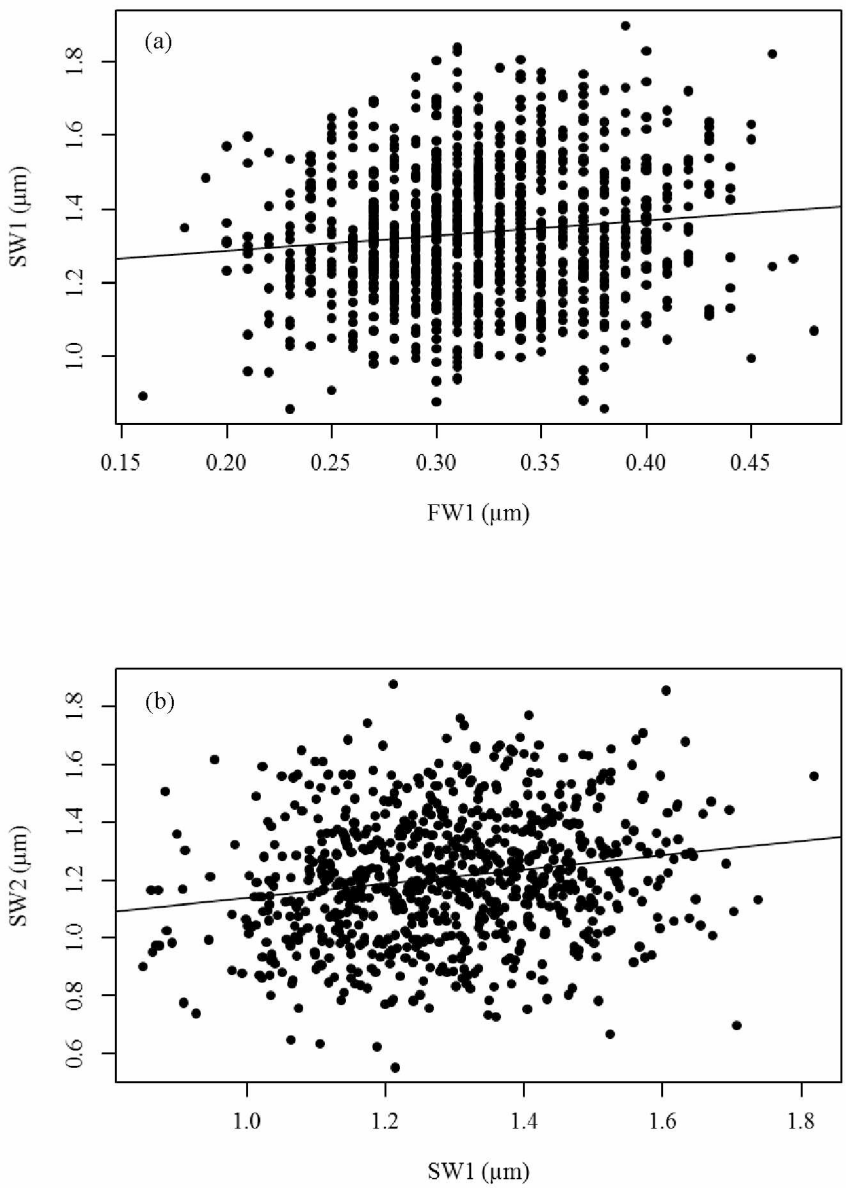

Figure 1.4. Scatter plots showing relationships between freshwater and first-year marine growth and between first- and second-year marine growth for (a) Chilkat River and (b) Stikine River Chinook Salmon. Soid lines represent linear relationships from linear regression models.

Table 1.1. Mean annual growth, range, and standard deviation of weighted annual growth zones for Chilkat and Stikine river female Chinook Salmon. Regression results were obtained from simple linear regressions between annual growth zones and brood year to test for linear trends over time (β, and its standard error, SE) using a t-test.

	Growth zone	Mean growth	Range	SD	β (*10^3)	SE (*10^3)	t value	p value
Chilkat River	FW1	0.32	0.29 - 0.35	0.01	0.51	0.50	1.02	0.32
	SW1	1.33	1.2 - 1.46	0.06	0.29	2.37	0.12	0.90
	SW2	1.16	1.09 - 1.31	0.06	0.97	2.29	0.44	0.66
	SW3	1.07	0.98 - 1.19	0.06	-0.97	2.26	-0.43	0.67
	SW4	0.87	0.7 - 1.06	0.09	-8.7	2.46	-3.54	0.002
Stikine River	FW1	0.33	0.31 - 0.34	0.01	-0.35	0.42	-0.83	0.42
	SW1	1.29	1.21 - 1.39	0.06	2.56	3.52	0.73	0.48
	SW2	1.21	1.09 - 1.37	0.09	-3.39	5.50	-0.68	0.51
	SW3	1.09	0.98 - 1.17	0.06	-2.58	3.54	-0.73	0.48
	SW4	0.77	0.66 - 0.84	0.05	0.04	3.06	0.013	0.99

Table 1.2. Weighted multiple and simple linear regression statistics performed to determine the relationships between annual growth zones and log-transformed recruitment benchmarks (total return, productivity, and marine survival) for Chinook Salmon from the Chilkat and Stikine rivers.

			Model				
	Dependent variable	Explanatory variable	β	SE	t value	P value	R^2
Chilkat River							
	Total Return	SW1	3.55	1.62	2.2	0.04	0.2
	Productivity	SW1	7.12	1.78	4.01	0.001	0.52
Stikine River							
	Total Return	SW1	-230.13	82.05	-2.81	0.02	0.71
		SW2	91.42	31.71	2.88	0.01	
	Productivity	SW1	7.36	3.02	2.44	0.03	0.31
	Marine Survival	FW1	51	19.79	2.58	0.04	0.85
		SW1	8.63	1.75	4.92	0.002	

Table 1.3. Results from one-tailed t-tests used to determine at which ages annual scale growth differs between age- 1.3 and 1.4 Chinook Salmon from the Chilkat and Stikine rivers. Percent difference is the difference in age-1.3 growth relative to 1.4 growth.

Growth zone	% difference	F-value	P value
Chilkat River			
FW1	2.7	8.11	0.005
SW1	5.1	46.51	<0.0001
SW2	11.2	101.8	<0.0001
SW3	10.2	52.82	<0.0001
Stikine River			
FW1	7.88	35.83	<0.0001
SW1	5.68	47.7	<0.0001
SW2	15.84	152.2	<0.0001
SW3	10.60	61.22	<0.0001

Chapter 2: Impact of biological and environmental factors on Chinook Salmon smolt migration run timing by brood year in the Chilkat River, Alaska[1]

Abstract

Downstream migration of anadromous salmon smolts varies across spatial and temporal scales due to differences in body size and environmental factors such as photoperiod, water temperature, and discharge. Despite the importance of migration timing and early marine entry on recruitment success, there is a lack of research on smolt migration cues for Alaska salmon stocks. This study utilized Chinook Salmon *Oncorhynchus tshawytscha* catch-per-unit-effort data from the Alaska Department of Fish and Game as a proxy for daily smolt migration trends and to create timing indices for the start, midpoint, and end of smolt outmigrations each year (sample years: 2002-2014). A generalized additive model (GAM) and multiple and simple linear regression were used to identify stimuli of daily trends and timing of Chinook Salmon smolt outmigration in the Chilkat River, Alaska. Daily smolt outmigration was positively correlated to water temperature and negatively correlated to discharge and the final model explained 68% of the deviance in daily CPUE. The start of the outmigration period (Julian day) was significantly negatively correlated with summer nearshore sea surface temperatures ($R^2 = 0.57$). The mid and end points of migration timing were positively correlated with smolt length ($R^2 = 0.72$ and 0.34, respectively). In general, more smolts migrated when discharge was low and water temperatures were warm, indicating that discharge may slow or halt migrations. The results indicate that both smolt length and growth rate influenced the outmigration timing of individual smolts, with large and small, fast-growing, individuals migrating earlier during the outmigration period. These results increase our understanding of environmental factors that influence the outmigration of Chinook Salmon in glacially fed rivers in Alaska and could be used as a baseline to guide future research.

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1 Berkman, S. A., T. M. Sutton, F. J. Mueter, M. D. Adkison, and B. W. Elliott. 2017. Impact of biological and environmental factors on Chinook Salmon smolt migration run timing by brood year in the Chilkat River, Alaska. Prepared for submission to Transactions of the American Fisheries Society.

Introduction

The migratory behavior of anadromous salmonids originated as a means to increase fitness (Gross et al. 1987). Fish that remain in freshwater ecosystems experience slower growth and lower fecundity but higher survival to reproductive age, whereas migrations to marine environments reduce the chances of survival while providing a higher quality and quantity of resources, increased growth opportunities, and greater fecundity (Gross 1987; Quinn 2005). The decision to migrate is species- and/or stock- specific, with significant variation in migratory patterns. Variation is attributed to localized population adaptations where migrations are dependent on fish body size and timed strategically so that fish experience optimal marine conditions to maximize growth and survival (Antonsson and Gudjonsson 2002; Spence and Hall 2010).

Early marine entry is a critical period in the life history of migrating salmonids and can determine recruitment strength (Beamish and Mahnken 2001; Mueter et al. 2005; Vega et al. 2017). Previous research on smolt migrations indicates that the large variability observed in marine survival may, in part, be due to migration timing and a match-mismatch with marine conditions and food availability (Hvidsten et al. 1998; Mortensen et al. 2000; Antonsson et al. 2010). Growth during early marine residency is related to marine survival, where increased growth improves the chance of surviving to reproductive maturity (Holtby et al. 1990; Mortensen et al. 2000; S. Berkman, UAF, unpublished data). Marine growth conditions are primarily influenced by water temperature and the availability of adequate prey resources (Brett et al. 1969; Mortensen et al. 2000). Smolts that outmigrate early in the season may be exposed to lower, less optimal sea surface temperatures (SST), increased predation pressure, osmotic stress, and limited food resources when they reach the ocean (Hvidsten et al. 1998; Mortensen et al. 2000; Rikardsen et al. 2004). Late migrating smolts may miss the spring zooplankton bloom and experience slower growth and size-selective mortality during their first winter at sea (Beamish and Mahnken 2001).

Before the transition from freshwater to the marine environment can occur, salmon parr must go through smoltification, which is a change in physiology and behavior to allow for survival in the marine environment (Healey et al. 1991; McCormick et al. 1998). Physiologically, smolts develop a tolerance for higher levels of salinity, lose their parr marks, turn silver in coloration, and increase their buoyancy (Saunders 1965; McCormick et al. 1998). Behavioral changes include increased downstream orientation, schooling, reduced territoriality, and higher salinity preference (Hoar 1988; Iwata 1995; McCormick et al. 1998). These changes are triggered by a combination of dynamic and static environmental cues, which fish use to detect and respond to ocean conditions (Quinn 2005).

Previous research has shown that shifts in photoperiod stimulate physiological changes, whereas environmental changes such as increased water temperature and river discharge trigger behavioral changes in migrating salmonid species (McCormick et al. 1998). Photoperiod is a consistent seasonal marker for a changing environment and activates the first parr to smolt transformations as well as increases their sensitivity to other environmental cues (Hoar 1976; McCormick et al. 1998). These environmental changes, which include increasing water temperature and discharge, can initiate and stimulate outmigration of some stocks (Bohlin et al. 1993b; Hvidsten et al. 1998; Antonsson and Gudjonsson et al. 2002). Although photoperiod stimulates smoltification, water temperature may control the rate of change by restricting smolt transformation at low temperatures (McCormick et al. 1998). Increases in water temperature act as a cue for migration, indicating optimal SSTs and increased food availability (Bohlin et al. 1993b; Mortensen et al. 2000). Increases in discharge may also influence outmigration timing and signal favorable stream migration or sea conditions. For example, Atlantic Salmon *Salmo salar* from southern Icelandic rivers halted migrations during high discharge from Arctic wind events, which were associated with declines in sea temperature, until discharge declined (Antonsson and Gudjonsson et al. 2002). In other stocks, high discharge stimulated migration by facilitating faster and more passive migration to the ocean (Bohlin et al. 1993a; Lawson et al. 2004). High discharge also increases turbidity, which can protect migrating smolts from visual-oriented predators (Bohlin et al. 1993a; Lawson et al. 2004). Overall, the relationships between environmental cues and outmigration are stock specific and vary due to differences in the reliability of these factors to signal optimal marine conditions (Antonsson and Gudjonsson 2002; Spence and Dick 2013).

Smolt body size can influence migration timing, with larger and faster-growing fish typically migrating earlier in the season than smaller, slower-growing individuals (Bohlin et al. 1993a, 1996; Antonsson et al. 2010). Larger smolts likely migrate earlier than smaller individuals because size-selective pressures linked to seaward migration oblige smaller fish to remain in freshwater to grow to a certain minimum size (Bohlin et al. 1996; Beamish and Mahnken 2001). In the ocean, larger individuals are more adept at escaping predation, can consume larger and more energy rich prey to meet metabolic demands, and are more tolerant of osmotic stress induced by low SSTs (Bohlin et al. 1996; Sogard 1997; Jensen et al. 2012). In some salmonid stocks, migration timing was related more to growth rate than absolute body size (Beckman et al. 1998). Fast-growing individuals with higher metabolic rates may migrate earlier and at a smaller body size because they become constrained by food limitations in freshwater systems earlier than their slow-growing conspecifics (Rikardsen and Elliott 2000).

Smolt migration timing is not dependent on a single factor, but a suite of interacting stimuli that are related to favorable marine conditions for fish survival to reproductive maturity (McCormick et al. 1998; Spence and Dick 2013). In northern regions, air temperatures are predicted to increase by 1 to 5°C over the next century, triggering shifts in freshwater thermal regimes, increased glacial melting, precipitation, and flooding, increased ocean temperatures, and a rise in sea level (Bryant 2009; Shanley and Albert 2014). These shifts are likely to influence freshwater growth rates, smolt migration timing, and marine survival in Pacific salmonids *Oncorhynchus* spp. due to an exacerbated match or mismatch between migration timing and the optimal smolt window (Holtby 1988; McCormick et al. 1998; Lawson et al. 2004). These climactic changes could be particularly detrimental to Pacific salmon stocks that are already experiencing reductions in production and survival.

In Alaska, Chinook Salmon *O. tshawytscha* are ecologically, culturally, and economically important and are currently facing increasingly low survival and high variability in stock recruitment (ADF&G Chinook Salmon Research Team 2013). Because the early marine entry period for Chinook Salmon from the Chilkat River in Southeastern Alaska (SEAK) has been identified as a critical period and a time of high mortality that can determine stock brood strength, it is important to understand the biological and environmental factors that influence smolt migration timing (Orsi et al. 2013). Although the importance of migration timing and early marine entry has been well documented for other salmon stocks, there is a lack of research on the stimuli that direct downstream smolt migrations in Alaska (Beamish and Mahnken 2001; Antonsson and Gudjonsson 2002). Therefore, the objectives of this study were to: 1) identify the relationship between daily smolt catch (as a proxy for daily migration) and smolt length, river temperature, discharge, photoperiod, and parental spawner abundance; and 2) determine how those variables influenced Chinook Salmon smolt outmigration timing in the Chilkat River.

Methods

Study site

The Chilkat River supports the fifth largest stock of Chinook Salmon in Southeastern Alaska, with a spawning run size of approximately 4,000 large (> 660 mm mid-eye fork length [MEF]) fish annually (ADF&G Chinook Salmon Research Team 2013). This stock was selected for this analysis because of its importance in Alaska and its status as one of twelve indicator stocks selected by the Alaska Department of Fish and Game (ADF&G). As an indicator stock, long-term and in-depth assessments have been conducted on this stock and, therefore, data exist for analysis. The Chilkat River is a glacial river that begins at the Chilkat Glacier in British Columbia, Canada, and drains into the Lynn Canal near Haines, Alaska (Figure 2.1; ADF&G Chinook Salmon Research Team 2013; Chapell and Elliott 2013). Harvest of Chilkat River Chinook Salmon is conducted through commercial troll, drift gill net, and purse seine fisheries, recreational fisheries, and local subsistence fisheries, with recent harvest rates approximately 16% of the total annual run (ADF&G Chinook Salmon Research Team 2013; Elliott and Power 2015). This stock has a stream-type life history, with the majority of the juveniles residing in freshwater for one year before migrating downstream as smolts. Based on Coded Wire Tag (CWT) recovery data, Chinook Salmon from this stock primarily rear in the northern inside waters of

Southeastern Alaska and Northern British Columbia (ADF&G Chinook Salmon Research Team 2013; Chapell and Elliott 2013).

Biological data

In 2000, a juvenile Chinook Salmon CWT survey was initiated to estimate parr and smolt abundance, smolt emigration, and marine harvest of the Chilkat River stock (Chapell 2013). Spring smolt sampling begins in April and is conducted entirely on the lower portion of the mainstem Chilkat River. Juvenile Chinook Salmon are captured using 100 gee minnow traps baited with disinfected salmon roe each day (Chappell 2013). All captured Chinook Salmon juveniles were injected with a CWT and held for 24 hours to ensure tag retention. Every 100th tagged fish was also measured for fork length (FL) to the nearest 1 mm and wet weight (to 0.01 g). Daily catch-per-unit-effort (CPUE; sample years 2002-2014) values were generated from the number of traps checked and Chinook Salmon captured each day. Daily CPUE values were used as a proxy for actual number of fish outmigrating that day to identify those factors that influence the number of smolts migrating on a given day. Chinook Salmon escapement data for the Chilkat River were acquired from the juvenile CWT study, and an adult mark-recapture study and used to define parental escapement of smolts from brood years 2000-2012 (Chapell and Elliott 2013). A term for the number of parental spawners was included in the model because it may influence annual variability in migration (Sykes et al. 2009).

In addition to daily estimates of CPUE, daily cumulative CPUE was used to determine the Julian day when 5, 50, and 95% of fish had migrated downriver, defining the start, midpoint, and the end of the lower river outmigration period, respectively. These dates were used to assess factors that have been shown to influence timing of smolt outmigration (Jonsson and Hansen-Rudd 1985). Although smolt sampling consistently began on or before April 10 each year and typically captured the entire smolt migration period, the migration started earlier than normal from 2004-2006. As a result, sampling efforts missed the start of the outmigration those years; therefore, analyses conducted using the start date (5% of fish that had migrated) for the outmigration included data from all years except 2004-2006.

Physical data

Environmental variables, such as water temperature and discharge, have been recognized as factors that influence salmon smolt outmigration and were included in this study (McCormick et al. 1998; Spence and Dick 2013). Daily river water temperature measurements (°C) were taken each day that Chinook Salmon were collected at 0900 hours over the entire time series (B. Elliot, ADF&G, unpublished data). To identify how water temperature influenced daily smolt migrations, temperature indices were created by averaging daily water temperature from April 12 (earliest date that water temperature data existed for all years) to the earliest midpoint (April 16) and the end date of outmigration (May 08) across all years. The temperature index could not be calculated for the start of the outmigration because water temperature data were not collected on that date for each year of the study. Previous research identified a significant negative relationship between mean spring river temperature and mean June and July SST from a station in Auke Bay near Juneau (Auke Bay Monitor AMB; S. Berkman, UAF, unpublished data). In lieu of river water temperature and because early marine conditions were important to the survival and growth of salmon, ABM SST was included in the analysis of outmigration start timing (Figure 2.1). Sea surface temperature data from ABM data were collected through the Southeast Alaska Coastal Monitoring (SECM) Survey which began in 1997 (Orsi et al. 2015). Sea surface temperature was sampled monthly in May, June, July, and August using a conductivity, temperature, and depth (CTD) Sonde at a depth of 3 m (Orsi et al. 2015). River discharge data were not available during the study period for the Chilkat River but do exist for three other nearby glacial-fed SEAK rivers. As a result, a discharge index for this region was created by averaging mean standardized daily discharges from the Taku, Stikine, and Antler rivers (m^3/s; 1998-2015) for the spring migration period (April 1- May 30). These rivers were chosen because they were the only glacial river systems in the region with data for the entire study period. These three rivers represented a wide range of drainage sizes (mean annual discharge from 2014-2016; Antler River: 4 m^3/s; Taku River: 401 m^3/s; Stikine River: 1,660 m^3/s). Discharge data from the United States Geological Survey (USGS) National Water Information System (http://www.usgs.gov/) was obtained as follows: Taku River near Juneau, Alaska (USGS gauging station #15041200), Stikine River near Wrangell, Alaska (USGS gauging station 15024800), and Antler River near Auke Bay, Alaska (USGS gauging station 15055500). Daily standardized discharge measurements were used with analyses on daily CPUE, and a cumulative discharge unit (CDU) was used for outmigration timing analyses. The CDU allowed seasonal trends in discharge to be accounted for and was the cumulative discharge from April 01 to the earliest start (April 06), midpoint (April 16), and end (May 08) date of outmigration over the study period.

Data analysis

Two separate analyses were conducted for this study: (1) temporal assessment of factors that influenced the daily number of smolts that outmigrated over the season; and (2) examination of the factors that influenced outmigration timing. To examine whether variability in daily CPUE was linked to short-term variations in biological or physical river conditions (analysis 1), daily CPUE data were used as the response variable and daily water temperature (°C), discharge (m^3/s), and average smolt fork length (mm) were used as explanatory variables. Preliminary analyses indicated that river water temperature, discharge, and Chinook Salmon smolt length all increased significantly over the sample period for each year in the Chilkat River (all $P < 0.001$). To focus on the short-term variability rather than the strong seasonal trends, the explanatory variables were detrended prior to analysis by removing the overall mean trend. Cross-correlation plots were examined to determine if lagged (lags 0-5) temperature or discharge would be better predictors of CPUE. Because the highest correlations generally occurred with temperatures and discharge on the same day, data that were not lagged were used in the analysis. Catch-per-unit-effort was modeled as a function of physical and biological conditions in the river including daily variability in detrended discharge, temperature, and smolt length using General Additive Models (GAM; conducted using the function "gam" in the "mgcv" package in R [Wood 2006; R Core Team 2014]).

Additive models were used to allow for potential non-linear relationships. However, smooth terms in the model were constrained to a maximum of three degrees of freedom to accommodate a range of biologically sensible relationships. To account for differences in mean CPUE resulting from variability in spawner abundance, the abundance of parental spawners that gave rise to the outmigrating smolts was included in the model as well. Exploratory analyses suggested that these variables could not account for longer-term (weekly to monthly) seasonal patterns, therefore a smooth seasonal trend was included in the model to account for any unexplained seasonal variability. Upon testing, there was no evidence (degrees of freedom close to 1) of non-linearities in the relationships with temperature and smolt length; therefore, the smooth terms were replaced with linear trends. A forward stepwise approach based on Akaike information criterion (AIC), which added terms one at a time based on the largest reduction in deviance, was used to select the top model (Table 2.1). Diagnostic plots were created to assess model fit and autocorrelation. The response variable, CPUE, was log transformed to improve model fit. Although there was some evidence of first-order autocorrelation, including autocorrelated residuals in the model did not improve the model fit substantially (higher AIC), therefore the original model (without a correlation term) was selected as the final model.

The analysis of migration timing was conducted using multiple and simple linear regression with Julian day when 5, 50, and 95% of smolts outmigrated each year as the response variables and the mean temperature, CDU, AMB SST, and smolt length for that period as explanatory variables. As a measure of smolt length for these analyses, the average length (mm) from April 12 to the earliest midpoint (April 16) and end date of outmigration (May 08) across all years were used. Mean smolt length could not be calculated for the start of the outmigration because these data did not exist on that date for each year in the study. A backward stepwise approach based on AICc (AIC with correction for small sample size) was used to select top models and reduced models were fit based on those selections.

Results

The full GAM indicated that CPUE was significantly related to discharge and water temperature but not smolt length or the number of parental spawners. The reduced model, excluding the non-significant terms, described 68.5% of the deviance in daily Chinook Salmon smolt CPUE (Figure 2.3; Table 2.2). Discharge was the most influential environmental factor for daily smolt CPUE which predominantly decreased as CPUE increased (Figure 2.3; Table 2.2). Water temperature was also significant in the model and was positively related to daily smolt CPUE.

Seasonal trends of the smolt outmigration varied over the study period (Figure 2.2). Two general outmigration patterns were distinguished within the sample period: (1) peak CPUE occurred in the beginning of the outmigration period and declined as season progresses and (2) CPUE peaked in the middle of the outmigration period. The first pattern was observed in sample years 2002-2006 and 2011. The second pattern was observed in sample years 2007-2010 and 2012-2014. The start of the Chinook Salmon smolt outmigration from the lower Chilkat River over the time series (2002-2014) began, on average, on Julian day 101 (April 10/11), and ranged from Julian day 96 (April 5/6) in 2013 and 2014 to Julian day 104 (April 13/14) in 2007 and 2008. On average, the midpoint occurred on Julian day 116 (April 25/26), and ranged from Julian day 106 (April 15/16) in 2005 to Julian day 127 (May 6/7) in 2007. The mean end date of outmigration was Julian day 135 (May 14/15), and ranged from Julian day 128 (May 7/8) in 2013 to Julian day 140 (May 19/20) in 2009.

Mean water temperatures for the midpoint and end of the outmigration period were 2.27 (range, 1.0 – 3.48°C) and 3.42°C (range, 2.26 – 5.10°C), respectively. Auke Bay Monitor SST data were only used in the model at the start of the outmigration period and the mean June and July SST over the time series was 12.6°C and ranged from 10.5 to 13°C. The average smolt length at the midpoint and the end of the outmigration was 72 (range, 67 – 78 mm), and 72 mm (range, 69 – 77mm), respectively. Smolt length, CDU, and AMB SST at the start of the outmigration period did not significantly change over the time series ($P = 0.15, 0.40, 0.10$, respectively). There were no significant temporal trends in any environmental or biological variables, except mean water temperature at the end of the outmigration period. Significant temporal trends were observed in water temperature at the end of the migration, with water temperatures declining over the time series (R^2= 0.37, P = 0.03).

The cumulative discharge unit and AMB SST in June and July were used to explain variation in the timing of the start of the smolt outmigration in the lower portion of the Chilkat River. Auke Bay Monitor SST was significantly negatively related to the start date of the outmigration (reduced model: R^2 = 0.57, P = 0.01; Figure 2.4; Table 2.3). Temperature, CDU, and smolt length at the midpoint of the outmigration period in the Chilkat River were used to explain midpoint migration variation over the time series. The fitted model indicated that there was a significant positive relationship between the midpoint of the smolt outmigration and smolt length (R^2 = 0.72, P = 0.0002; Figure 2.4; Table 2.3). Water temperature, CDU, and smolt length at the end of the smolt outmigration period were fitted in a multiple linear regression model to explain variation in the timing at the end of the outmigration period over the time series. Smolt length was the only explanatory variable significantly related to the timing at the end of the outmigration and smolt length was longer in years that outmigrations ended later (R^2 = 0.34, P = 0.04; Figure 2.4; Table 2.3)

Discussion

This study indicated that fine-scale daily Chinook Salmon smolt movements in the Chilkat River appear to be influenced by water temperature and discharge during the outmigration period. Although photoperiod was not a factor included in this study, it has been well recognized as a priming factor that influences smolt migration and may contribute to Chinook Salmon smolt outmigration (McCormick et al. 1998; Spence and Dick 2013). Previous studies have suggested that seasonal changes in photoperiod stimulate the physiological changes associated with smoltification and increase pre-smolt sensitivity to other environmental cues (Hoar 1988; McCormick et al. 1998). Sykes et al. (2009) examined outmigration of Chinook Salmon in British Columbia and observed that although photoperiod likely initiates smoltification, it did not affect migration behaviors. Saunders et al. (1985) reared Atlantic Salmon at two light regimes (i.e., constant and natural) and determined that fish in each sample grew to a similar size, with fish in the constant light regime not undergoing smoltification. Reliance on photoperiod by salmonids as an environmental cue of optimal marine conditions is also stock specific and may depend on the variability or stability of other environmental stimuli. Spence and Hall (2010) and Spence and Dick (2013) suggested that Coho Salmon *O. kisutch* in Alaska relied more on photoperiod as an indicator of favorable marine conditions than stream temperature and discharge because the latter exhibited greater interannual variability than photoperiod. Further, increases in photoperiod and light levels in northern areas, like SEAK, are linked to the spring primary production and zooplankton blooms (Stabeno et al. 2004; Spence and Hall 2010). Coho Salmon stocks in the Pacific Northwest may be more responsive to changes in stream temperature and discharge as migration cues because they may be stronger predictors of ocean upwelling and increases in ocean production (Spence and Hall 2010). In the Chilkat River, photoperiod may be used by Chinook Salmon smolts as a general indicator of optimal marine conditions, while more dynamic changes (i.e., temperature and discharge) stimulate finer-scale daily movements as cues of localized optimal times for migration and nearshore conditions.

Daily water temperature was significantly related to daily CPUE of Chinook Salmon smolts in the Chilkat River, with greater CPUE occurring at higher water temperatures. Chinook Salmon in the Chilkat River exhibited a short migration period over a wide range of water temperatures, indicating there was no specific temperature that triggered migration. However, over the time series, the majority of Chinook Salmon smolts were captured when water temperatures ranged between 3-4°C, suggesting that these temperatures are ideal for outmigration and may relate to optimal SSTs for growth in the marine environment. Similarly, the outmigration of Brown Trout *S. trutta* smolts in a Norwegian river was positively related to water temperature, with the majority of fish migrating between 6-10°C (Hembrel et al. 2001). Previous research has indicated that the influence of water temperature on smolt outmigration varies with latitude because of differences in spring water temperature patterns and their reliability to relate to sea conditions in northern versus southern regions (Antonsson and Gudjonsson 2002; Jensen et al. 2012). For Coho Salmon, protracted smolt outmigrations observed for southern stocks (e.g., Oregon) were likely related to the slow increase in spring water temperatures over many months. In the north (SEAK), Coho Salmon exhibited short outmigration periods, similar to Chinook Salmon in the current study, likely in response to rapid changes in spring water temperatures and high variability in those temperatures over the season (Spence and Dick 2013). The current study also observed that while the end of outmigration timing varied annually, migrations consistently ended before water temperatures reached 7°C. This suggests that there may be a thermal maximum that stimulated remaining smolts to migrate (Antonsson and Gudjonsson 2002).

A significant negative relationship was detected between the start of outmigration and June/July SSTs at Auke Bay Monitor. Smolt outmigrations began earlier in years when nearshore summer SSTs were also warmer, indicating the presence of an in-river factor that stimulated outmigration based on regional warming as indicated by SSTs. Previous research on Chinook, Coho, and Atlantic Salmon showed that early smolt outmigrations occurred during years with warmer spring air and river temperatures (Antonsson and Gudjonsson 2002; Lawson et al. 2004; Sykes et al. 2009; Spence and Dick 2013). Alternatively, in the Chilkat River, Chinook Salmon smolt may be responding to decreases in river water temperature, as a significant negative relationship was detected between summer AMB SST and average water temperature over the outmigration period (S. Berkman, UAF, unpublished data). Because the Chilkat River is a glacially fed system, the dynamics of the relationship between SST, river temperature, and smolt outmigration are complex and unlike those reported previously in the literature. Smolt outmigrations are believed to occur at times that will maximize growth and survival in the marine environment and, therefore, typically coincide with increased SSTs and food production (McCormick et al. 1998; Antonsson and Gujonsson 2002). Primary production in SEAK is likely correlated to increased day length and photoperiod, with the spring zooplankton bloom following at a short lag (Stabeno et al. 2004). In glacially fed rivers, warmer air temperatures and greater solar radiation lead to increased glacial melt and discharge, which reduces overall river water temperature during this period (Milner and Petts 1994). Increased air temperature and solar radiation also increases SSTs and, therefore, lower water temperature in glacially fed systems may trigger migration and act as a reliable cue related to favorable marine conditions.

Discharge is commonly identified as a major influence of smolt outmigration (McCormick et al. 1998). Hembrel et al. (2001) determined that anadromous Brown Trout in a Norway river migrated more frequently during increased discharge periods even though discharge did not necessarily initiate migration. The authors suggested that changes in overall river conditions associated with discharge were likely responsible for the onset of migration. In a study on geographically distinct Coho Salmon stocks, only weak relationships between discharge and migration probability were identified for the Sashin Creek, Alaska, stock while increased migration probability was associated with short-term increases in flow when stream discharges were not already high in southern Coho Salmon stocks (Spence and Dick 2013). These contrasting results could indicate that discharge may be inconsistently related to ocean conditions in some areas and not regularly relied upon by salmonids. In the current study, discharge was the most significant environmental variable in the model. High daily discharge was correlated with low CPUE, which may indicate that fewer fish migrated during periods of high flow. Similarly, a negative relationship was identified between river discharge and migration probability for Chinook Salmon in Nechako River, British Columbia (Sykes et al. 2009). Despite this negative relationship, the authors speculated that an increase in discharge was beneficial because it facilitated migration rates. Hvidsten et al. (1995) also determined that discharge was the most important factor that influenced the smolt outmigration of Atlantic Salmon, and detected a positive relationship between outmigration and discharge. For the Chilkat River, marine survival was lower during years with higher mean spring discharges (S. Berkman, UAF, unpublished data). High spring discharge in SEAK rivers may augment migration rates to a point and potentially increase migration survival, but trigger or force smolts to migrate at a time that subjects them to suboptimal marine conditions. Lawson et al. (2004) suggested that similar mechanisms regulated patterns in migration and survival for Coho Salmon in Oregon where higher spring flows increased migration survival but were associated with later spring transitions and poor marine conditions. Chinook Salmon in the Frasier River, British Columbia, also exhibited reduced survival in years with high discharge because increased river inputs into the Strait of Georgia caused increased turbulence, reduced stability, and low production in nearshore estuarine areas (Gargett 1997). In addition, the current study detected no significant relationships between discharge and smolt outmigration timing. Discharge may stimulate day-to-day outmigrations, but is likely not reliable or stable enough of an environmental cue to stimulate larger scale outmigration timing trends (Lawson et al. 2004).

Chinook Salmon smolt body length did not significantly influence daily trends or the timing of the start of the smolt outmigration in the Chilkat River. However, there were significant positive relationships between the timing at the midpoint and end of the outmigration period and smolt length. These results may indicate that smolts remain in freshwater for longer periods if resources and conditions are optimal for growth. Research on Chinook Salmon in the Chilkat and Stikine rivers found that smolt body size was significantly related to marine survival (S. Berkman, UAF, unpublished data). Larger individuals tend to have higher survival rates due to lower gape limitations, fewer predators, faster swimming rates, and higher tolerances of suboptimal marine conditions (Holtby et al. 1990; Bohlin et al. 1996; Sogard 1997). Increased time spent in freshwater and larger size upon outmigrating may increase the survival of Chinook Salmon in the Chilkat River. In addition, the current study, mean smolt length over the time series was identical at the midpoint and the end of the outmigration period. Previous research on smolt outmigration relative to body size indicates that larger fish typically migrated first and smaller individuals remained in freshwater to grow in a safer environment (Bohlin et al. 1993a; 1996). Ewing et al. (1984) detected similar results for Chinook Salmon smolts in the Deschutes River, Oregon, where fish size remained constant over the outmigration period, indicating larger fish migrated first and smaller fish remained in freshwater to attain a minimum size before initiating outmigration. This size-based difference in outmigration timing was likely related to survival advantages in the marine environment when fish were larger.

Although there was evidence that suggests, on average, larger smolts outmigrated earlier than smaller conspecifics, the observed increase in daily smolt length over the sampling period suggests absolute body length was not the only biological factor stimulating seaward migration. Jensen et al. (2012) also detected an increase in smolt body size over the primary migration period for Atlantic Salmon, Brown Trout, and Arctic Char *Salvelinus alpinus* in Norway and suggested that individual fish growth rate may be more important to outmigration timing. Smaller, but faster-growing, individuals may be the first to become constrained by food limitations in freshwater and migrate earlier to increase growth opportunities in the ocean (Beckman et al. 1998; Rikardsen and Elliott 2000; Jensen et al. 2012). In addition, some of the observed increases in smolt body size over time may be a result of the greater duration for freshwater growth exhibited by later outmigrants. Antonsson et al. (2010) determined that longer and later migrating smolts had the highest survival rates in two Icelandic Atlantic Salmon stocks. The large range in smolt body size observed at the midpoint and end of outmigration may indicate that both absolute body size and individual growth rate were functioning simultaneously to stimulate outmigration in different individuals. The importance of larger smolt body size at outmigration has been observed for stocks when marine conditions and survival were below average (Holtby et al. 1990; Woodson et al. 2013; Graham 2016). Alternatively, Vega et al. (2017) observed an increase in growth rate and size in Chum Salmon that migrated to sea earlier, which may indicate a survival advantage for individuals that migrate early, regardless of body size. Although these relationship were unclear for Chinook Salmon in the Chilkat River, smolt body size and growth rate could become significant with climate change as environmental migration cues change and mismatches increase between migration time and optimal marine conditions.

The catch-per-unit-effort data used in this study was acquired through baited minnow trap sampling. The goal of the sampling on the Chilkat River was to capture and tag (CWT) as many fish as possible for the mark-recapture study (Chapell 2013). Because minnow traps are effective in the capture of small fish they are widely used in tagging studies. However, the effectiveness of minnow traps is related to placement site and daily variability in catch can be based on location, not actual number of fish outmigrating (Hi and Lodge 1990). In addition, trap effectiveness can be influenced by discharge, where high discharge creates velocity barriers around the trap and reduces catch (Portt et al. 2006). The biases associated with minnow trap catch data may have influenced results in the current study. Previous research on smolt outmigrations have used more standardized sampling methods including weirs and rotary-screw traps, which are stationary traps that are not influenced by daily sampler placement and less impacted by changes in environmental conditions (Sykes et al. 2009; Spence and Dick 2012). Although data were limited in the current study, the methods and results may act as a first step in understanding the downstream smolt outmigration of Chinook Salmon in SEAK.

These study results highlight the variability in the stimuli and timing of the Chinook Salmon smolt outmigration in the Chilkat River, Alaska. Smolt outmigration from the lower Chilkat River appears to be influenced by in-river mechanisms that related to nearshore sea conditions in the summer. The correlations observed between the timing of the start of outmigration and June and July AMB SSTs suggests that temperature was a major factor influencing outmigration timing. Discharge may have also influenced timing in conjunction with temperature and limited daily outmigrations at high discharges. The patterns observed between smolt size and outmigration suggest that both smolt body size and growth rate influenced outmigration timing. Migration timing has also been shown to influence marine survival in Chinook and Coho Salmon in Oregon and Alaska, Pink Salmon *O. gorbuscha* in Auke Bay, Alaska, and Atlantic Salmon in Iceland (Mortensen et al. 2000; Lawson et al. 2004; Antonsson et al. 2010; S. Berkman, UAF, unpublished data). Because of the strong relationships observed between marine survival and migration timing, an increased understanding of environmental factors that influence outmigration could allow managers to make more reliable management forecasts. Regional similarities in outmigration patterns have been found in some stocks and may be apparent in glacially fed Alaskan rivers. As a result, identifying these similarities in Alaska should increase our understanding of Chinook Salmon declines throughout Alaska (Antonsson and Gudjonsson 2002; Spence and Dick 2013).

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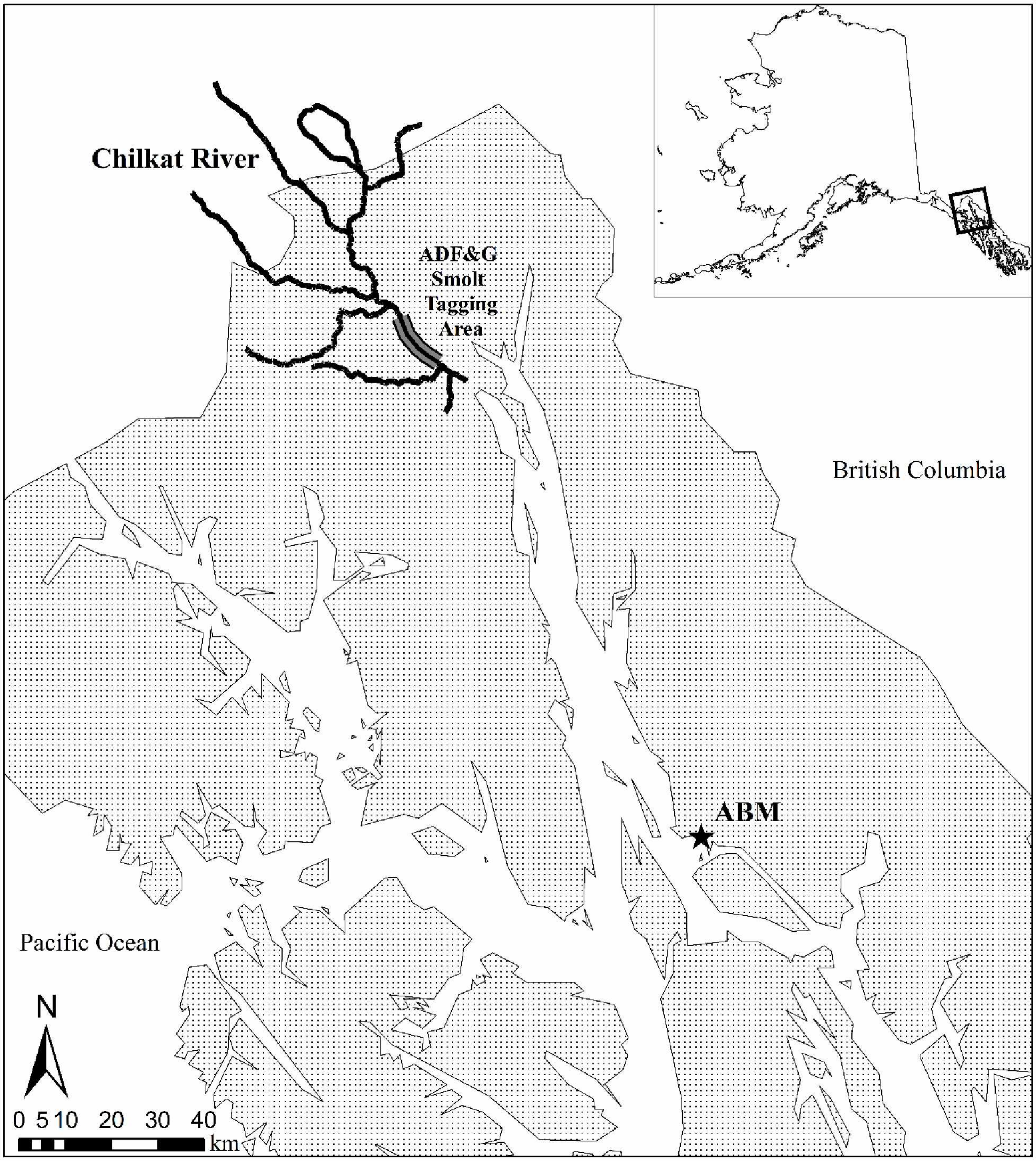


Figure 2.1. Map of the Chilkat River in Southeastern Alaska. The dark line indicates the location of the Chilkat River, the gray shading indicates the transect that ADF&G sampled smolts in the spring, and the star indicates the location of Auke Bay Monitor where SST data were collected.

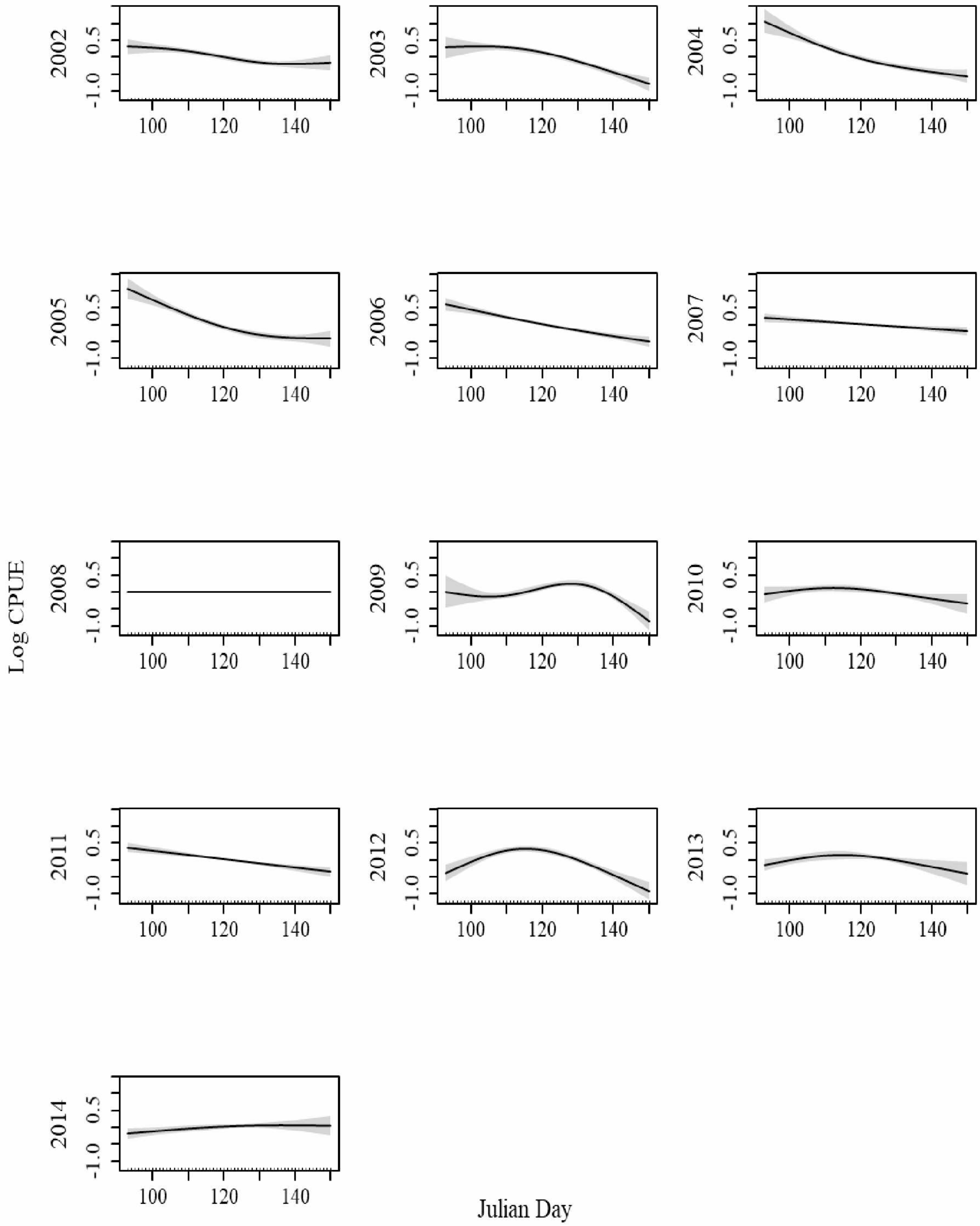
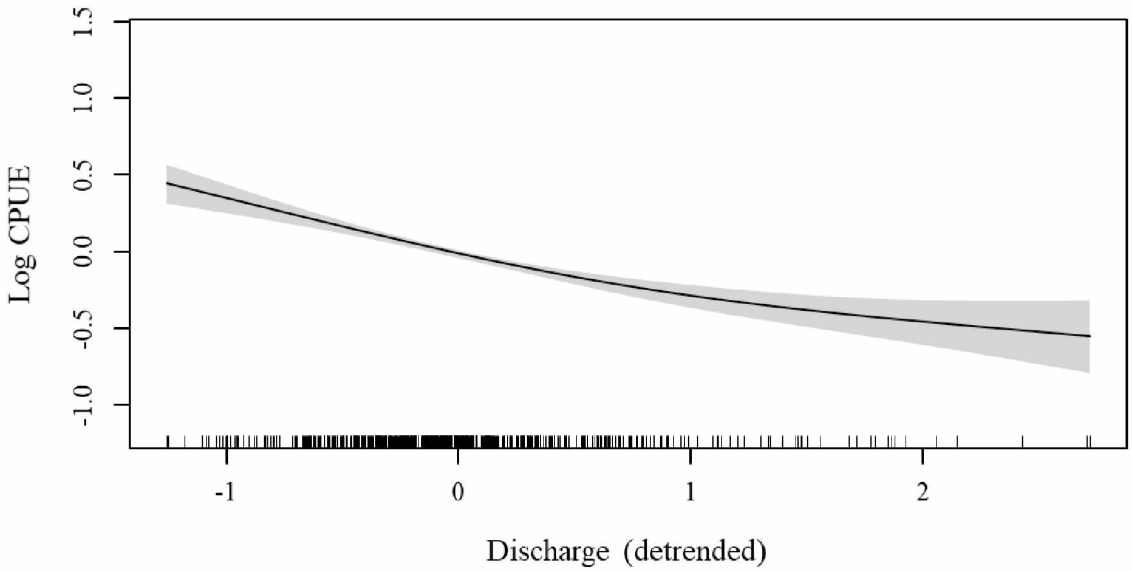


Figure 2.2. Catch-per-unit-effort of Chinook Salmon smolt by Julian date for each sample year (2002-2014). Black lines represent smooth function (k=3) and gray bands represent confidence intervals for each year in the study period.

a



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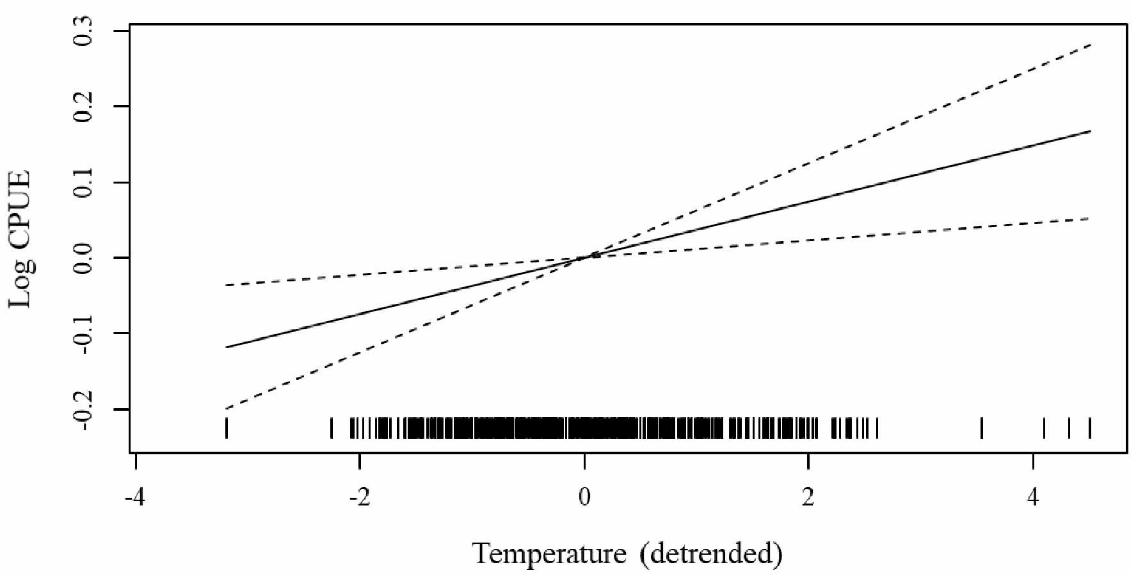

Figure 2.3. The smooth and linear relationships between daily CPUE and (a) discharge and (b) temperature, respectively. Bars on the bottom of each plot represent concentration of data points. Black lines represent smooth (a) and linear (b) trend lines and the gray and dotted bars represent confidence intervals.

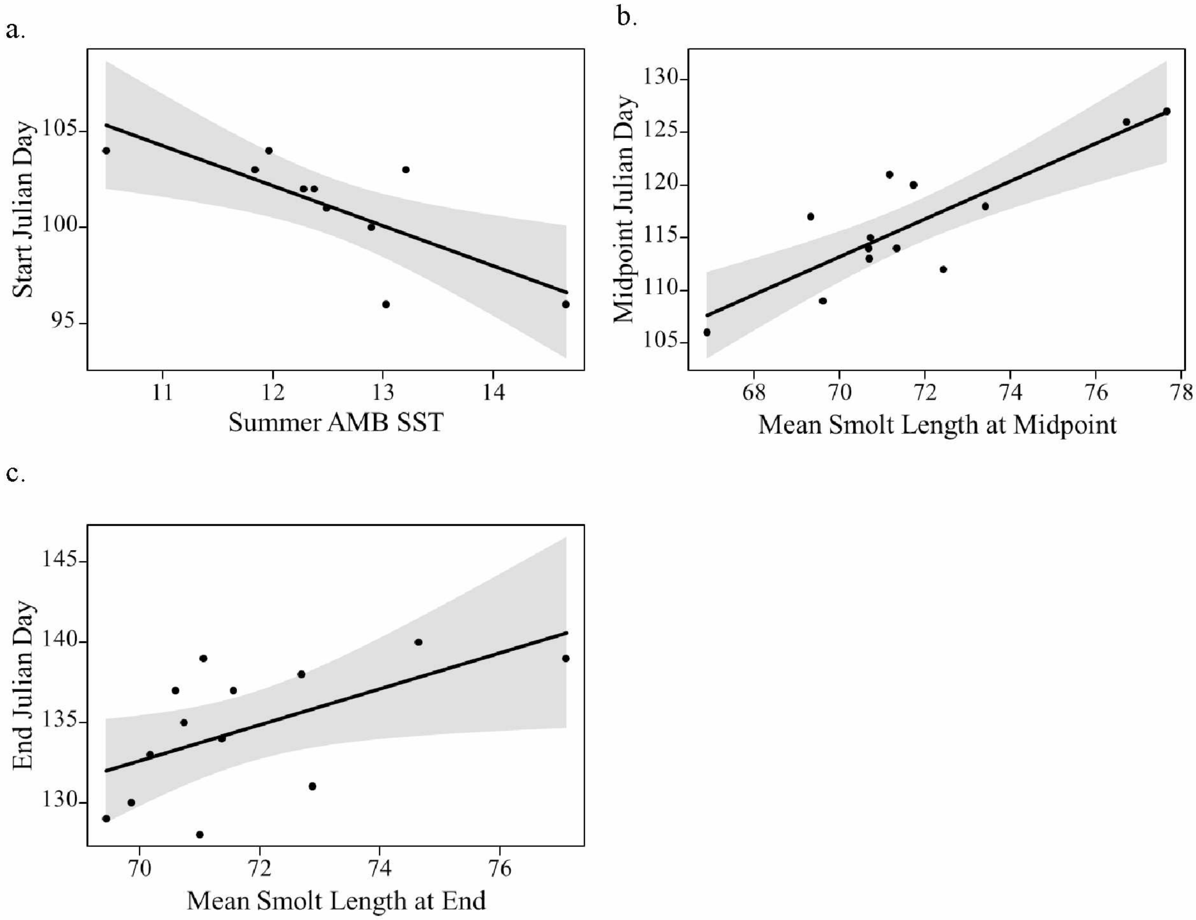

Figure 2.4. Linear relationships between Chinook Salmon (a) start of smolt outmigration and summer AMB SST and the (b) midpoint and (c) end of Chinook Salmon smolt outmigration and mean smolt length. Black bars represent significant linear trends and gray bands are confidence intervals.

Table 2.1. Stepwise GAM fits between daily CPUE of Chinook Salmon smolts in the Chilkat River, Alaska, and biological and environmental explanatory variables. Bolded model represents the final selected model.

Additions	Gam	AIC	%	Change in % deviance	Residual d.f.	Residual deviance	Change in deviance
Null	0	546.73	0		594	86.73	
sJulian	1	161.85	52	52	570.29	41.59	-45.14
Year	2	-21.45	66.3	14.3	557.38	29.21	-12.38
sDischarge	3	-69.74	68.7	2.4	559.45	27.16	-2.05
Temp	**4**	**-74.15**	**69.1**	**0.4**	**557.9**	**26.77**	**-0.39**
Smolt ln	5	-72.25	69.1	0	556.96	26.76	-0.01
Spawners	6	-72.24	69.1	0	556.97	26.76	0

Table 2.2. Results from the top GAM between daily CPUE of Chinook Salmon smolts in the Chilkat River, Alaska, and biological and environmental explanatory variables. Statistic represents t-test for temperature and F-tests for year, and the smooth terms of discharge and Julian day.

Explanatory Variable	d.f.	Coefficient	Statistic	P-value
Year	12		29.67	< 0.001
Temperature	1	0.04	2.91	0.004
s(Discharge)	2.24		29.53	< 0.001
s(Julian)	21.6		15.81	< 0.001

Table 2.3. Results from the selected linear regression models of timing of Chinook Salmon smolt outmigration start, mid, and end point and biological (smolt length) and the environmental (AMB SST) explanatory variable.

Migration Timing		Model				
Dependent Variable	Explanatory variable	B	Standard error	t-value	P-value	R-squared
Start	AMB SST	-2.09	0.63	-3.29	0.01	0.57
Midpoint	Smolt Length	1.8	0.34	5.35	0.0002	0.72
End	Smolt Length	1.13	0.475	2.37	0.04	0.34

Chapter 3: Effect of Chinook Salmon early life stage biological attributes and environmental factors on survival to reproductive maturity in Southeastern Alaska Rivers[1]

Abstract

Highly variable recruitment and declines in productivity and abundance of Chinook Salmon *Oncorhynchus tshawytscha* have created economic and cultural hardships for communities throughout Alaska. As a result, it is necessary to better understand factors influencing freshwater and marine survival and production of Chinook Salmon stocks. This study utilized principal component analysis (PCA) and principal component regression (PCR) to determine how parr length, fall and spring air temperature, and discharge influenced freshwater overwinter survival and smolt production in the Chilkat River (brood years [BY] 1999-2009). Multiple and simple linear regression and PCA and PCR were used to determine the influence of smolt body size (i.e., length and weight), June and July sea surface temperatures (SST), spring discharge and river temperature, and migration timing on marine survival in the Chilkat River (BY 1999-2009) and in the Stikine River (BY 1998-2009). Freshwater smolt production had a significant negative relationship with parr length and fall discharge ($P = 0.05$) and a significant positive relationship with spring temperature and discharge ($P = 0.03$), indicating lower fall discharge, and higher early spring temperatures and discharge increase smolt production in the Chilkat River. The negative relationship between smolt production and parr length indicated density dependent growth in freshwater. Marine survival of Stikine River fish was significantly related to smolt length, indicating that brood marine survival was higher when smolts were larger ($R^2 = 0.26$). For the Chilkat River, marine survival was significantly correlated to a principal component that loaded primarily on migration timing, smolt length, and discharge, with greater marine survival occurring in years when smolt migrations were completed later in the season, smolt migration was longer, and discharge was lower ($R^2 = 0.5$). These results support the importance of the early marine period in determining year-class strength and highlight the variation in mechanisms that influence survival of Chinook Salmon stocks.

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1 Berkman, S. A., T. M. Sutton, F. J. Mueter, M. D. Adkison, B. W. Elliott. 2017. Relationship between Chinook Salmon early life stage biological attributes and environmental factors on survival to reproductive maturity in Southeastern Alaska Rivers. Prepared for submission to Transactions of the American Fisheries Society.

Introduction

Pacific salmon *Oncorhynchus* spp. survival varies with each life stage. Identifying critical periods of high mortality that determine brood strength can lead to more narrow and directed analyses on biotic and abiotic factors that may affect stock during these periods. Although life-history strategies of salmonids vary by species and stock, most fish go through single or multiple freshwater overwintering periods before migrating to the marine environment (McCormick et al. 1998; Quinn 2005). As a result, freshwater overwinter and early marine entry periods are frequently recognized as critical periods in the life history of Pacific salmon (Holtby et al. 1990; Beamish and Mahnken 2001; Neuswanger et al. 2014).

In freshwater, parr must survive at least one overwintering period, which is characterized as a high stress period with freezing water temperatures, low river discharge, surface ice, and low productivity (Biro et al. 2004; Huusko et al. 2007). Previous research indicates that overwinter survival of juvenile salmonids is related to body size, with larger individuals having higher survival rates than their smaller conspecifics (Hunt 1969; Smith and Griffith 1994; Zabel and Achord 2004). Larger, faster-growing individuals can better escape size-selective survival pressures, such as predation, and have a larger gape size, which allows for the consumption of a greater diversity of larger, higher-energy prey (Houde 1987; Sogard 1997; Thompson and Beauchamp 2014). Larger fish typically have greater lipid reserves and a lower relative metabolic rate, which helps to sustain them during winter months (Biro et al. 2004; Thompson and Beauchamp 2014). A larger body size may also enable these individuals to secure higher quality overwintering habitats (Quinn and Peterson 1996; Biro et al. 2003; Zabel and Achord 2004).

Environmental conditions before, during, and after the overwintering period can also influence overwinter survival (Hunt 1969; Cunjak 1988; Lawson et al. 2004). Low water temperatures reduce metabolic costs of salmonids, and also reduce their feeding efficiency, predator avoidance capability, and ability to respond to environmental changes such as shifting ice (Huusko et al. 2007; Hurst 2007; Brown et al. 2011). These stressors can cause metabolic deficits that lead to starvation or increased predation mortality due to forage-based risk-taking behavior (Cunjak 1988; Biro et al. 2003). Acclimation costs linked to shifting water temperatures that occur in the fall and spring can also result in depletions of lipid reserves and lower body condition, which can limit survival during longer winter periods (Cunjak et al. 1987). Reductions in discharge during winter can also limit overwintering habitats and displace parr during low discharge events (Lawson et al. 2004). High winter discharge events can stress river ice, which creates cracks that can fragment and lead to fish mortality events (Huusko et al. 2007; Brown et al. 2011). Extreme high discharge events can also flush parr from overwintering habitats and restrict areas for effective drift foraging (Lawson et al. 2004; Neuswanger et al 2014). Increases in turbidity as a result of high discharge can further reduce the foraging ability of parr by limiting visibility, but can also protect fish from visual predators (Lawson et al. 2004; Neuswanger et al. 2014). Finally, higher flows can increase available overwintering habitat, increase carrying capacity, and reduce competitive interactions among juveniles (Lawson et al. 2004).

Following the overwintering period, parr undergo behavioral and physical changes as they undergo smoltification and become better adapted to living in a marine environment (Healey et al. 1991). Early marine entry is a critical period for juvenile Pacific salmon that can determine brood-year (BY) recruitment strength (Beamish and Mahnken 2001; Mueter et al. 2002b; Quinn 2005). Movements of salmon smolts from freshwater to marine waters are based on the evolutionary concept of risk and reward, which suggests that it is energetically advantageous yet riskier to migrate to and feed in the ocean than it is to remain in resource-limited freshwater habitats (Jonsson and Jonsson 1993; Quinn 2005). Previous research on smolt migration indicates that large variability in marine survival may, in part, be due to migration timing and a match-mismatch between smolt arrival, sea conditions, and food availability (Rikardsen et al. 2004; Hvidsten et al. 2009; Antonsson et al. 2010). Migration timing has been linked to smolt body size (e.g., with larger or faster-growing smolts migrating first) and environmental changes (e.g., photoperiod, water temperature, discharge; Bohlin et al. 1993; Antonsson et al. 2010; Vega et al. 2017). Environmental changes, such as increases in water temperature, trigger migratory movements, whereas discharge may augment migration as higher flows enable a more passive transportation downstream (Bohlin et al. 1993; McCormick et al. 1998; Lawson et al. 2004).

Correlations between body size, early marine growth, and survival have been found for Chinook Salmon *O. tshawytscha*, Coho Salmon *O. kisutch*, Sockeye Salmon *O. nerka*, Pink Salmon *O. gorbuscha*, and Atlantic Salmon *Salmo salar* (Holtby et al. 1990; Koenings et al. 1993; Mortensen et al. 2000; Antonsson et al. 2010; Murphy et al. 2013). The critical size, critical period hypothesis states that the majority of natural mortality in the marine environments for Pacific salmon occurs during two periods: (1) predation in the early marine period; and (2) mortality of fish smaller than a critical size due to their inability to meet minimum metabolic requirements during their first year at sea (Beamish and Mahnken 2001). Larger, faster-growing individuals are able to capture larger prey at an earlier age, which can lead to improved metabolic efficiency and greater growth (Quinn 2005). Similar to freshwater survival, larger individuals deplete their energy reserves less rapidly than smaller fish and are better equipped to survive periods of starvation (Sogard 1997; Beamish et al. 2004; Biro et al. 2004).

Ocean conditions and associated variability during the early marine period can influence survival as well (Nickelson 1986; Mueter et al. 2002b; Jutila et al. 2005; Mueter et al. 2005). Fish typically have a specific optimal temperature or range of temperatures for growth, which is species and region specific, where metabolic rate is most efficient and growth is maximized (Wootton 1998). Regional ocean conditions, such as sea surface temperature (SST), may influence and represent an array of conditions, including upwelling and prey abundances and distributions; in turn, these conditions may benefit or hinder salmon growth and survival (Cole 2000; Mortensen et al. 2000; Mueter 2002a, b). Large-scale climate indicators have been linked to salmon survival, with warmer conditions in the Pacific Ocean favoring Alaskan salmon stocks while cooler conditions favor southern stocks (Mantua et al. 1997; Cole 2000; Mueter et al. 2002a). Finer-scale regional SST data have also been used and may be better predictors than large-scale indicators (Mueter et al. 2002a). Juvenile body size during the early marine period has been shown to be more influential during years when mortality was high and marine survival was below average, indicating that large body size was more important when marine conditions were suboptimal for growth and survival (Holtby et al. 1990; Woodson et al. 2013; Graham et al. 2016).

Although previous research has demonstrated the importance of body size and environmental conditions to the freshwater and early marine survival of Pacific salmon stocks, the factors influencing variability in recruitment and survival of many Chinook Salmon stocks in Alaska remain unknown. Chinook Salmon support important and diverse subsistence, commercial, recreational, and personal use fisheries throughout the state. In Southeastern Alaska (SEAK), Chinook Salmon stock declines, increased variability in recruitment, and historical overharvest over the past 60 years have led to fishing restrictions for Chinook Salmon as well as other Pacific salmon species. These restrictions, in turn, have created cultural, social, and economic hardships for many communities in this region (ADF&G Chinook Salmon Research Team 2013). With impending threats, including climate change and mine development, it is imperative to understand the basic mechanisms that have affected the survival and recruitment of these stocks. The objectives of this study were to: 1) uncover influences of biological (parr length) and environmental (temperature and discharge) factors on freshwater overwinter survival and smolt production of Chinook Salmon in the Chilkat River, Alaska; and 2) determine how biological (smolt body size, smolt migration timing) and environmental (regional SSTs, river discharge, river temperature) factors influenced marine survival of Chinook Salmon in the Chilkat and Stikine rivers in SEAK. This research will provide a better understanding of the factors that influence freshwater overwinter and marine survival of Chinook Salmon stocks and provide managers with the necessary information to develop more accurate and reliable forecasts for Chinook Salmon in SEAK.

Methods

Study sites

The Chilkat and Stikine rivers were selected for this study because they support important regional Chinook Salmon stocks, long-term data exists for both systems, and impending threats may expose these stocks to future declines. These rivers are two of the twelve indicator tributaries selected by the Alaska Department of Fish & Game (ADF&G) and Department of Fisheries and Oceans Canada (FOC, [for transboundary stocks]) to be sampled and studied for in-depth stock assessments (ADF&G Chinook Salmon Research Team 2013). This monitoring program was initiated due to state-wide and regional declines in Chinook Salmon stocks and the need for increased information to be used in run forecasting (ADF&G Chinook Salmon Research Team 2013). The Chilkat River is a moderately sized, glacially fed river that originates at the Chilkat Glacier in British Columbia, Canada, and drains into the Lynn Canal near Haines, Alaska (Figure 3.1; ADF&G Chinook Salmon Research Team 2013; Chapell and Elliott 2013). This river supports the fifth largest stock of Chinook Salmon in SEAK, with a spawning run size of about 4,000 large (> 660 mm mid-eye fork length [MEF]) fish annually (ADF&G Chinook Salmon Research Team 2013). The Stikine River is a transboundary river originating in British Columbia that drains into the ocean near Wrangell, Alaska (Figure 3.1). Chinook Salmon in this river are jointly managed by ADF&G and FOC (Jaecks et al. 2015). The Stikine River supports the second largest stock of Chinook Salmon in SEAK, with a spawning run size of approximately 22,000 large (> 660 MEF length) fish annually (Pahlke 2010; ADF&G Chinook Salmon Research Team 2013). Chinook Salmon in both rivers have a stream-type life history, where juveniles reside in freshwater for one year before migrating downstream as age-2 smolts (Quinn 2005; ADF&G Chinook Salmon Research Team 2013).

Biological data

Chinook Salmon marine survival (Chilkat River brood years [BYs]: 1999-2009; Stikine River BYs: 1998-2009), smolt abundance, and smolt biological attributes (fork length [mm]) were estimated for the Stikine and Chilkat River using spring coded wire tag studies (CWT; 2000-present) and adult mark-recapture programs (Chilkat River: 1991-present; Stikine River: 1996-present) by ADF&G (Chapell and Elliott 2013; Elliott and Power 2015; Jaecks et al 2015). Overwinter survival, parr abundance, and parr biological attributes (fork length [mm]) were only available for the Chilkat River (BYs 1999-2009) and were measured as part of the ADF&G fall CWT program (Elliott and Power 2015). Estimates of total annual smolt abundance were used to represent freshwater smolt production.

Data from the spring CWT sampling program in the Chilkat River were used to create smolt migration timing indices (Chapell and Elliott 2013). Minnow traps were set and checked daily in the upper and lower reaches of the Chilkat River to tag the maximum number of fish (Chapell and Elliott 2013). The number of minnow traps set and Chinook Salmon catches were used to calculate the daily catch-per-unit-effort (CPUE) over the spring sampling period (early April-late May) for both reaches. The daily CPUE of the lower Chilkat River was used as a proxy for the total number of fish migrating to the ocean each day. To capture differences in annual migration timing and develop temporal indices, the Julian date when 95% of smolts had been captured was used to define the end of outmigration.

Physical data

Overwinter Survival

For overwinter survival of Chinook Salmon in the Chilkat River, data were lagged to represent experienced environmental conditions in the fall and spring. River discharge data were not available for the Chilkat River during sample years 2000-2010 (BY 1999-2009). Therefore, a proxy for Southeastern Alaska discharge based on the combined standardized mean monthly discharge from the Taku, Stikine, and Antler rivers (1998-2015) for fall (September-November) and early spring (March-April) was used. These rivers were chosen because they were the only glacial river systems in the region with data for the entire study period. These three rivers represented a wide range of drainage sizes (mean annual discharge from 2014-2016; Antler River: 4 m^3/s; Taku River: 401 m^3/s; Stikine River: 1,660 m^3/s) and were all significantly related to each other. Discharge data from the United States Geological Survey (USGS) National Water Information System (http://www.usgs.gov/) was obtained as follows: Taku River near Juneau, Alaska (USGS gauging station #15041200), Stikine River near Wrangell, Alaska (USGS gauging station 15024800), and Antler River near Auke Bay, Alaska (USGS gauging station 15055500). Although discharge during winter may also affect overwinter survival (Lawson et al. 2004), USGS rated discharge measurements from ice-covered rivers as poor and rivers in SEAK are typically ice covered from December-early March and (Brian Elliott, ADF&G, personal communication; M. Kang, USGS, personal communication). Long-term monthly stream temperature data were not available for the Chilkat River. However, air temperature data did exist for a National Oceanic and Atmospheric Administration (NOAA) station close to the Chilkat River; Haines 40 NW (GHCND:USC00503504), in Klukwan, Alaska (https://www.ncdc.noaa.gov). Because strong correlations exist between stream temperature and air temperature above freezing (0°C), air temperature was used as a proxy for stream temperatures (Mohseni and Stefan 1999). These indices comprise means of daily air temperature from the Haines 40 NW station from September-November (fall) and March-April (spring). Although the relationship between air and water temperature may be different for glacially-fed streams, the air temperature indices used in these analyses likely captured the annual variation in temperature conditions. The fall and spring periods were chosen because of their importance to pre-smolt salmonids (Cunjak et al. 1987).

Marine Survival

For analyses of Chinook Salmon marine survival in the Chilkat and Stikine rivers, SSTs from the inshore marine waters of Southeast Alaska (°C) were acquired from the National Oceanic and Atmospheric Administration (NOAA) for 1997-2015. These data were collected through the Southeast Alaska Coastal Monitoring (SECM) Survey which began in 1997 (Orsi et al. 2015). Sea surface temperature has been sampled monthly from May through August using a conductivity, temperature, and depth (CTD) Sonde at a depth of 3 m at three different locations (Figure 3.1; Orsi et al. 2015). These sampling locations represented inshore (Auke Bay Monitor) and strait (Upper Chatham Strait, Icy Strait) rearing habitats (Orsi et al. 2015). Because SEAK Chinook Salmon migrate to the marine environment from April-late May, an index of marine entry SSTs was developed by averaging the SSTs for all stations during June and July (Pahlke et al. 2010; Chapell and Elliott 2013; Orsi et al. 2015). This index was lagged by two years (BY + 2 years) to match the time when each BY would enter the ocean.

River conditions during smolt outmigration were also used in the analysis of marine survival. Average river temperature (Chilkat River only) and river discharge at the time of outmigration (April-May) can affect run timing and early ocean conditions experienced by smolts. River temperature data were only available for the lower Chilkat River and were collected by ADF&G during the CWT smolt sampling program (2001-2011; Chapell and Elliott 2013). Daily temperatures were averaged for each sample year to develop an overall spring river water temperature variable. River discharge data were available for the Stikine River through a USGS gauging station (15024800) near Wrangell, Alaska (http://www.usgs.gov/). The SEAK discharge proxy, explained above, was adapted and used in Chilkat River analyses. A spring migration period discharge index was developed for both rivers by averaging monthly mean discharge (SEAK index on standardized scale) from April-May, the primary migration period for Chinook Salmon smolts.

Data analysis

The influence of biological and environmental factors on overwinter survival and smolt production of Chinook Salmon in the Chilkat River was determined through principal component analysis (PCA) and principal component regression (PCR). Due to small sample sizes (N = 11), a large number of explanatory variables (N = 6), and multicollinearity between variables, PCA and PCR were most appropriate for these analyses. The environmental explanatory variables were lagged to represent conditions experienced by fish during their first fall prior to overwintering in freshwater (BY+1) and during the following spring during outmigration (BY+2). Both parr length and environmental variables (fall and spring discharge, fall and spring air temperature) were included in a correlation matrix and new linear combinations of the data were created using PCA with varimax rotations (Jackson 2005). The rotated principal components (PCs) which accounted for the greatest amount of variability were chosen through a visual assessment of a scree plot. Principal component regression models were fitted to test for significant relationships between response variables (log-transformed overwinter survival and smolt production) and PCs.

Similar analyses (PCA in combination with PCR) were used to estimate effects of biological and environmental factors on marine survival of Chinook Salmon in the Chilkat River. For Chilkat River analyses, log-transformed marine survival was used as the response variable and three PC variables combining spring river temperature and discharge, summer SST, Julian date of the end of smolt outmigration, and smolt length were included as explanatory variables. Environmental and run timing variables were lagged (BY+2) to represent conditions and run timing experienced by that BY. For Stikine River analyses, multiple and simple linear regression were used to test for significant relationships between log-transformed marine survival and spring discharge, SST, and smolt length. Preliminary exploration of variables included in the Stikine River analyses indicated the presence of possible outliers, therefore robust regression analyses were used (conducted using the function "lmRob" in the "robust" package in R [R Core Team 2014]). To select the best model for these data a backward stepwise approach based on the Akaike Information Criterion for small sample sizes (AICc), which removed terms one at a time based on largest reduction in deviance, was used to select top models. All statistical analyses were conducted in R 3.2.2 (R Core Team 2014).

Results

Overwinter survival and smolt production

Over the available time series (BY 1999- 2009), mean freshwater overwinter survival for Chinook Salmon in the Chilkat river was 36% and ranged from 21% for BY 2000 to 53% for BY 2005 (Figure 3.2). Mean smolt abundance was 172,616 fish, and ranged from 105,300 smolts (2000) to 282,700 smolts (2003; Figure 3.2). There was no significant linear trend over time in overwinter survival (R^2 = 0.12, P = 0.29), smolt abundance (R^2 = 0.05, P = 0.49), or parr length (R^2 = 0.0001, P = 0.97). Mean parr length was 69 mm, ranging from 64 mm (2006) to 74 mm (2005), and had a significant negative relationship with parr abundance (R^2 = 0.54, P = 0.01; Figure 3.2).

Discharge was similar over the study period in fall, and both higher and more variable in spring. Mean fall temperature was 3.16°C (range, 2.15 – 4.80°C) and mean spring temperature was -0.83°C (range, -3.81 – 2.5°C). There were no significant temporal trends in discharge or temperature data (fall and spring discharge: $P = 0.45$ and $P = 0.86$, respectively; fall and spring temperature: $P = 0.93$ and $P = 0.74$, respectively).

Two PCs were retained for the analyses because they accounted for a majority of the variation in the dataset. The first PC (PC1) loaded most heavily on parr length and fall discharge and intermediately on early spring temperature, while PC2 loaded most heavily on early spring discharge and early spring temperature (Table 3.1). The PCR model indicated that the two PCs explained little of the variation in overwinter survival ($R^2_{adj} = 0.14$, $F = 1.78$, $P = 0.23$). There were no significant relationships between overwinter survival and PC1 or PC2 ($P = 0.12$ and $P = 0.51$, respectively; Table 3.1). Both PC1 and PC2 were significantly correlated to smolt production with PC1 negatively correlated ($ß = -0.1$, $P = 0.05$) and PC2 positively correlated ($ß = 0.19$, $P = 0.03$, $R^2_{adj} = 0.52$), implying enhanced smolt production when discharge was lower in the previous fall and when discharge was higher and temperatures were warmer in the spring (Figure 3.2; Table 3.1). The negative relationship between smolt production and PC1 also indicates high smolt production limits parr size.

Marine survival

Over the time series (BY 1999 – 2009), mean marine survival of Chinook Salmon in the Chilkat River was 2.8% and ranged from 1.3% (BYs 2002 and 2008) to 4.7% (BY 2000; Figure 3.3). Although not significant, there was a negative temporal trend in marine survival in the Chilkat River ($R^2 = 0.34$, $P = 0.06$). For the Stikine River, mean marine survival was 1.7% (range, 0.56% in BY 2004 to 3.9% in BY 2000). There was no significant temporal trend in marine survival in the Stikine River ($R^2 = 0.08$, $P = 0.36$; Figure 3.3).

Annual mean length for Chinook Salmon smolts in the Chilkat and Stikine rivers were 73 mm (range, 69 - 79 mm) and 74 mm (range, 70 – 81 mm), respectively. There were no significant trends in smolt length over the study period in either river. Mean summer SST over the study period was 12.1°C and ranged from 10.5°C to 13°C. Mean Chilkat River temperature during the spring migration period

(April-May) was 4.3°C (range, 3.3 – 5.5°C), and there was no significant temporal trend over this time period ($P = 0.16$). Mean spring discharge for the Stikine River was 1,147 m^3/s (range, 679 – 1574 m^3/s) and there was no significant temporal trend in these data ($P = 0.23$). On average across brood years, the smolt outmigration in the Chilkat River ended on Julian date 136 (May 15/16), and the end date ranged from Julian day 129 (May 8) in 2004 (BY 2002) to day 143 (May 23) in 2001 (BY 1999). The peak of the downstream smolt outmigration occurred, on average, on Julian day 111 (April 20/21), and ranged from Julian day 98 (April 8) in 2006 (BY 2004) to day 130 (May 10) in 2007 (BY 2005). Outmigration timing was correlated with both environmental and biological variables. The date of the end point of outmigration was positively correlated to smolt length ($r = 0.73$) and negatively correlated to spring discharge ($r = -0.69$).

Three PCs were retained and were used to explain variation in log-transformed marine survival of Chinook Salmon on the Chilkat River. The first PC (PC1) loaded heaviest on migration timing, smolt length, and discharge, the second PC (PC2) loaded primarily on SST, and the third PC (PC3) loaded heaviest on average river temperature (Table 3.2). The log-transformed marine survival of Chinook Salmon in the Chilkat River was significantly negatively correlated to PC1, implying a positive relationship between the Julian date at the end of the outmigration period and smolt length and marine survival and a negative relationship between spring discharge and marine survival ($R^2 = 0.5$, $P = 0.01$; Figure 3.3). For Stikine River Chinook Salmon, the log-transformed marine survival was significantly positively correlated to smolt length ($R^2 = 0.26$, $P = 0.05$; Figure 3.3). There were no significant relationships observed between marine survival and SST or spring discharge and therefore, neither was included in the final model.

Discussion

The relationship between smolt production and fall discharge in the Chilkat River demonstrated the influence that discharge can have on freshwater survival of Chinook Salmon. Lawson et al. (2004) found that survival and smolt production was limited by low winter discharge, which likely reduced overwinter habitat availability. The current study found that lower fall discharge levels were associated with increased smolt production. Previous research on juvenile stream-type Chinook Salmon in the Yukon River, Alaska, found that high discharge during the summer was related to low production, possibly because high discharge caused velocity barriers that limited safe drift-foraging habitat and increased risk-taking behaviors induced by foraging (Neuswanger et al. 2014). High spring flows have been found to improve survival during smolt outmigration because higher discharge is associated with increased turbidity, which could protect fish from visual predators (Lawson et al. 2004). In the current study, smolt production was positively related to early spring discharge conditions which may indicate that pre-migrants benefited from turbidity-induced predator protection as well. Higher early spring flows could also increase habitat and drift-feeding opportunities while reducing competitive interactions between juvenile salmonids (Lawson et al. 2004). The positive relationship between smolt production and early spring discharge shown in the current study could also indicate an advantage when the winter period is shorter and spring thaw occurs earlier.

Previous research has found that warmer winter temperatures improve overwinter survival of salmonids (Hunt 1969; Smith and Griffith 1994; Meyer and Griffith 1996). Hunt (1969) and Smith and Griffith (1994) found that the overwinter survival of juvenile Brook Trout *Salvelinus fontinalis* and Rainbow Trout *O. mykiss* in Wisconsin and Idaho, respectively, was higher when winter temperatures were milder. Acclimation costs linked to changing water temperatures that occur in the fall and spring can result in the depletions of lipid reserves and lower body condition, which may reduce survival during longer winters (Cunjak et al. 1987). The current study found that Chinook Salmon smolt production increased with warmer early spring temperatures, which could reflect a survival advantage when winter periods are shorter and are followed by warmer spring water temperatures. In contrast, Lawson et al.

(2004) related air temperature to freshwater production of Coho Salmon in Oregon and found lower smolt production occurred during years with higher annual temperatures.

Juvenile body size can also influence freshwater survival and production of salmonids. Previous research has found that larger body size increased overwinter survival and production because higher lipid reserves enabled larger individuals to tolerate harsh winter conditions, increased size-based predator avoidance abilities, and competitive advantages over smaller individuals for quality habitats (Meyer and Griffith 1996; Quinn and Peterson 1996; Zabel & Achord 2004). The current study found that higher smolt production was related to smaller Chinook Salmon parr body size, which may indicate density dependence in the freshwater rearing environment. Armstrong and Griffiths (2001) found that the proportion of overwintering Atlantic Salmon sheltering decreased with abundance. In the Chilkat River, higher densities could have reduced the scope for growth for individual Chinook Salmon due to competition for food or habitat refugia. Small size may also be beneficial in some systems and years. Carlson and Letcher (2003) observed that older, larger salmonids had lower survival than younger, smaller individuals. The authors suggested that this relationship may be due to larger fish being more habitat limited in the winter and therefore more susceptible to predation. Good et al. (2001) found that smaller Atlantic Salmon fry had higher survival during summer floods than larger individuals, possibly because smaller fish were able to use small velocity refuges or shallow riffle pool habitats.

Previous research on the marine survival of Pacific salmon has emphasized the importance of the early marine period on determining BY strength (Holtby et al. 1990; Beamish and Mahnken 2001; Mueter et al. 2002; Quinn 2005). Although different factors influenced marine survival of Chinook Salmon in the Stikine and Chilkat rivers, these results reiterated the importance of the early marine period. Marine survival was higher in BYs when mean smolt length was longer in the Chilkat and Stikine rivers. Size-selective processes that influence marine survival are commonly observed in Pacific salmon. Recent research on Chinook Salmon in the Yukon River found that early marine mortality was high for the smallest juveniles in the population (Murphy et al. 2013). Koenings et al. (1993) found that smolt-to-adult survival increased with smolt size for Sockeye Salmon in Alaska, and demonstrated that this relationship was due to differences in behaviors of smaller versus larger smolts. Larger smolts had higher survival rates because they emigrated offshore and were able to better capture pelagic zooplankton, whereas smaller smolts remained in less productive nearshore areas. The relationship between smolt size and marine survival in these two rivers also highlights the importance of the freshwater period and the freshwater conditions that allow for more growth and larger smolt sizes.

Smolt outmigration timing has been shown to be stock specific and correlated with optimal local marine conditions (Hvidsten et al 1998). Optimal conditions led to fish experiencing favorable SSTs for growth, increased food resource abundance, and/or reduced predator interactions (Hvidsten et al. 1998; Mortensen et al. 2000). In the current study, the end date of outmigration was positively related to the marine survival of Chinook Salmon in the Chilkat River. Brood years where the smolt outmigration ended later in the season exhibited higher marine survival. Antonsson et al. (2010) also found that Atlantic Salmon that migrated later had higher survival, while Mortensen et al. (2000) found that the earliest and latest emigrating Pink Salmon smolts had the lowest marine survival rates. Early outmigrants experienced colder water temperatures and lower prey densities, which likely resulted in lower survival. For Chilkat River Chinook Salmon, migrations that end later may have provided additional time for some smolts to attain a larger size before outmigration or may have spread smolts out over a wider range of conditions, increasing the chance that some encountered favorable marine conditions.

Increased spring discharge during outmigration has been found to influence migration timing and may also be linked to marine survival. For Chinook Salmon smolts in the Nechako River, British Columbia, high discharge and river temperatures resulted in shorter migration periods (Sykes et al. 2009). Lawson et al. (2004) found that high spring discharge could facilitate outmigration by increasing swimming speed and allowing fish to be transported downstream more passively, potentially conserving energy reserves and improving survival. High spring discharge also results in greater turbidity which can protect smolts from visual predators (Lawson et al. 2004). The current study found that higher spring discharge resulted in earlier outmigrations and lower marine survival for Chinook Salmon from the Chilkat River. This relationship may indicate that optimal ocean conditions, prey densities, and/or predation pressure for these fish occurred later and early spring discharge events triggered smolts to migrate too early. Further, body size has been found to influence migration timing, where larger smolts migrate first followed by smaller fish (Bohlin et al. 1993; Antonsson et al. 2010). In the current study, body size and migration timing were correlated, with smaller smolts being captured earlier than larger smolts. Similar results were found for Atlantic Salmon, Brown Trout, and Arctic Char *Salvelinus alpinus* and may indicate that smaller, but fast-growing individuals were the first to become constrained by food in freshwater and migrate early to increase growth in the more productive marine environment (Jensen et al. 2012). Alternatively, the greater duration of freshwater growth for later outmigrants could be directing this pattern.

Local SSTs were not related to marine survival of Chinook Salmon from the Stikine and Chilkat rivers. Mortensen et al. (2000) found that higher SSTs in Auke Bay were related to higher growth and survival of Pink Salmon from Auke Creek, Alaska. Increases in survival related to SSTs stem from optimal growth conditions as temperature is the primary function that controls metabolic and growth rates for ectotherms (Brett et al. 1969; Groot et al. 1995). Sea surface temperatures can also impact ocean conditions, such as upwelling, food availability, and predator assemblages, all of which may aid or hamper Pacific salmon growth and survival (Cole 2000; Mortensen et al. 2000; Mueter et al. 2002a, 2005). Mueter et al. (2005) found that warmer coastal SSTs were associated with increased survival for Chum *Oncorhynchus keta*, Sockeye, and Pink Salmon in Alaska. Similar results were found for Chinook Salmon in the Unuk River, Alaska, with higher marine survival occurring with higher coastal SSTs (Graham 2016). The lack of a relationship between nearshore SSTs and Chinook Salmon marine survival in the Stikine River could be due to the majority of individuals rearing elsewhere. Chinook Salmon from the Stikine River are thought to rear in more open ocean areas and it is possible that most smolts migrate directly to the Gulf of Alaska or the Bering Sea rather than staying in nearshore areas. Alternatively, marine survival of Chinook Salmon from the Chilkat River, believed to rear in nearshore waters, was correlated to migration timing and river conditions, but not nearshore SSTs. Trawl surveys conducted during the summer in nearshore areas in SEAK by Orsi et al. (2013) determined that CPUE of ocean-age-1 Chinook Salmon from the Chilkat River was significantly correlated with marine survival, indicating BY strength was determined within the first year of ocean residence. The authors also found very few ocean-age-0 Chinook Salmon in the summer trawls, which suggests these fish may be non-migratory upon marine entry and remain in more localized areas. Brood-year marine survival was higher in years when discharge was lower during smolt outmigration. River conditions may be more indicative of the environment experienced by smolts when a large portion of marine mortality occurs. For example, Chinook Salmon smolts from the Fraser River fared worse during years when discharge into the Strait of Georgia was high because it caused increased turbulence, reduced stability, and low production in the estuarine areas (Gargett 1997). High seasonal discharge levels may cause similar patterns in the nearshore areas in SEAK where Chinook Salmon from the Chilkat River rear and therefore limit survival.

The results of this study indicated that environmental mechanisms influencing survival of Chinook Salmon in SEAK were stock-specific. Spring river conditions and outmigration timing appeared to influence marine survival of Chinook Salmon in the Chilkat River, but not in the Stikine River. These differences may be a result of the differences in rearing locations of the stocks. Smolt length appeared to influence survival in both the Stikine and Chilkat rivers. Results from this study also reiterated the importance of environmental and biological factors on freshwater production and early marine survival for determining brood strength of Pacific Salmon stocks. Although there was no evidence in this study that parr size influenced the overwinter survival of Chinook Salmon in the Chilkat River, the negative relationship between smolt production and parr length indicated density-dependent mechanisms occurred during freshwater rearing. River conditions also influenced smolt production, smolt outmigration timing, and marine survival in the Chilkat River. Warmer water temperatures and increased discharge projected by climate change may impact freshwater production and marine survival if mismatches between feeding and growth conditions are exaggerated in both freshwater and marine systems. This study provided SEAK fisheries managers with insights into the factors influencing freshwater production and marine survival of two important Chinook Salmon stocks and these results may help improve the accuracy and reliability of forecasts for stocks in this region.

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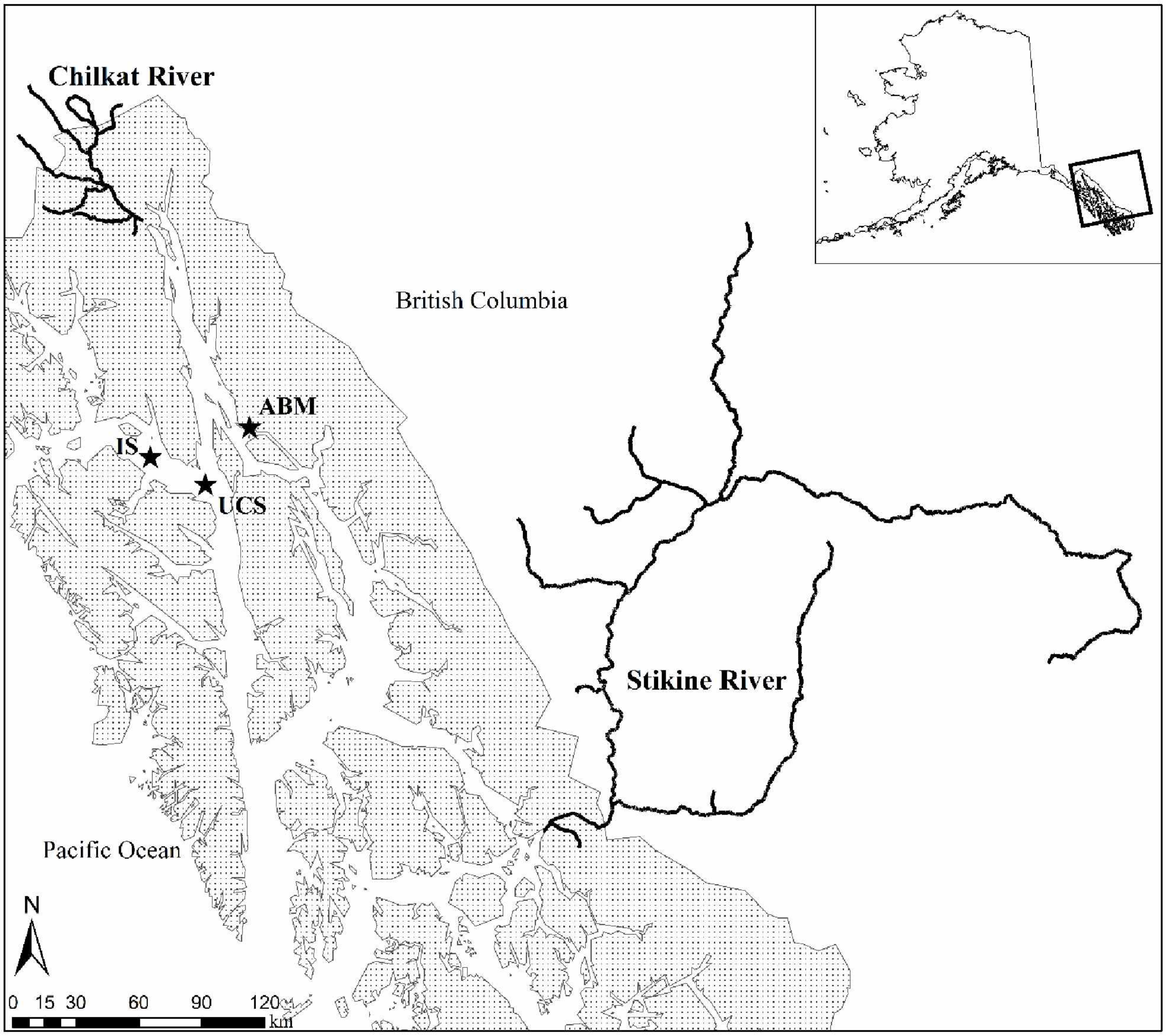

Figure 3.1. Locations of the Chilkat and Stikine rivers in Alaska and British Columbia. The stars indicate collections locations for Auke Bay Monitor (ABM), Upper Chatam Strait (UCS), and Icy Strait (IS) SST data.

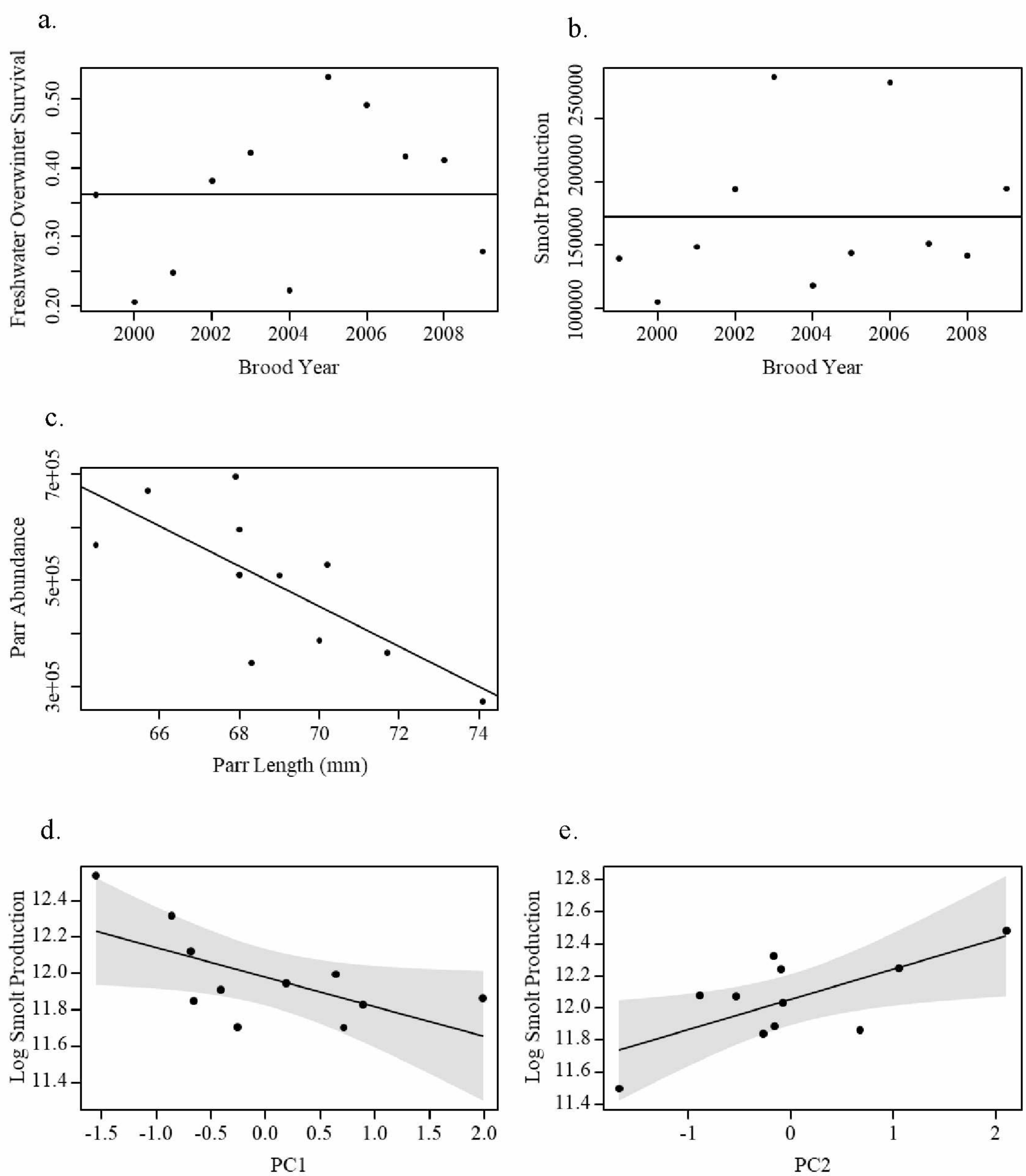

Figure 3.2. Temporal relationships among freshwater (a) overwinter survival and (b) smolt abundance by brood year, (c) relationship between parr abundance and parr length, and the relationships between log-transformed smolt production and (d) PC1 and (e) PC2 for Chinook Salmon in the Chilkat River, Alaska. The horizontal lines in the first two plots indicate mean freshwater overwinter survival and smolt abundance. The line in (c) is based on a regression of parr length on parr abundance. The lines and gray bands in (d and e) are the regression lines and confidence intervals, respectively, based on the PCR of PC1 and PC2 on smolt production.

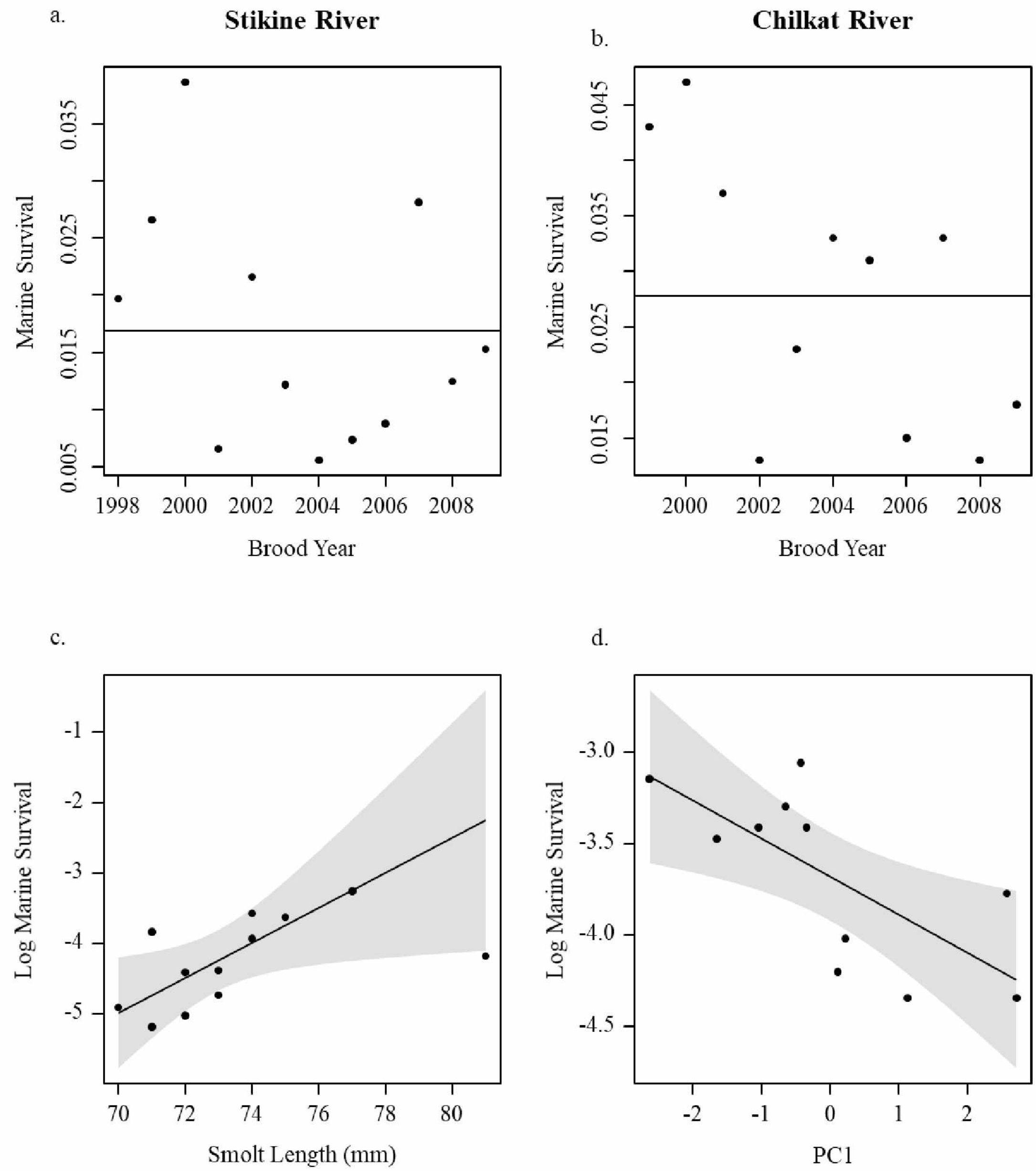

Figure 3.3. Time series of marine survival for the (a) Stikine and (b) Chilkat rivers. The horizontal lines represent mean survival for the two rivers for all sample years (BY 1998-2009 and BY 1999-2009 for the Stikine and Chilkat rivers, respectively). Bottom plots show relationships between log-transformed marine survival and smolt length for the (c) Stikine River and the relationship between log-transformed marine survival and PC1 for the (d) Chilkat River with regression lines and confidence interval bands.

Table 3.1. Loadings of the (a) rotated PCA used to model relationships with overwinter survival and smolt production. Results from (b) PCR model between PCs and overwinter survival and smolt production for Chinook Salmon on the Chilkat River.

(a)	PC 1	PC2	PC3
Parr length	0.95	-0.23	
Fall discharge	0.87	0.15	0.3
Spring discharge	0.19	0.91	0.13
Fall temperature	0.13	0.12	0.98
Spring temperature	-0.37	0.89	
Proportion explained	0.4	0.37	0.23
Cumulative proportion	0.4	0.77	1

(b)		Model				
Dependent variable	Independent variable	B	SE	t value	P value	R^2
Freshwater overwinter survival	PC1	0.07	0.09	0.69	0.51	0.14
	PC2	0.17	0.09	1.8	0.12	
Smolt production	PC1	-0.16	0.07	-2.31	0.05	0.52
	PC2	0.19	0.07	2.7	0.03	

Table 3.2. Loadings for selected principal components from a PCA of environmental and biological variables for the Chilkat River.

Dependent variables	PC1	PC2	PC3
Migration Timing	-0.54	0.33	-0.1
SST	0.25	0.85	0.002
Smolt Length	-0.49	0.31	-0.29
Spring discharge	0.53	0.27	0.24
Spring River Temperature	-0.36	0.06	0.92
Proportion explained	0.54	0.22	0.15
Cumulative proportion	0.54	0.75	0.91

Table 3.3. Results from the final PCR and linear regression models between log-transformed marine survival and PC1 and smolt length for the Chilkat and Stikine rivers, respectively.

		Model				
Dependent Variable	Independent variable	B	Standard error	t-value	P-value	R-squared
Chilkat River						
Marine survival	PC1	-0.21	0.07	-3.03	0.01	0.5
Stikine River						
Marine Survival	Smolt Length	0.25	0.11	2.18	0.05	0.26

General Conclusions

This study has expanded our understanding of the biological and environmental factors that influence growth and recruitment strength of Chinook Salmon stocks in Southeastern Alaska (SEAK). In chapter one, the importance of annual growth in determining the marine survival, total return, and productivity was assessed for two regionally important Chinook Salmon stocks. Annual growth during the first year at sea was positively and significantly related to recruitment benchmarks in both the Chilkat and Stikine rivers. Freshwater growth was also positively related to marine survival of Chinook Salmon from the Stikine River. Evidence of growth dependency between freshwater and first-year marine growth from the Chilkat River and between first- and second-year marine from the Stikine River was observed as well. The growth of age-1.3 fish began to exceed that of age-1.4 fish during the freshwater rearing period in both stocks. The second chapter characterized the downstream smolt outmigration and examined biological and environmental factors that explained annual variation in the outmigration timing of Chinook Salmon from the Chilkat River. Variations in the daily catch-per-unit-effort (CPUE) of Chinook Salmon smolts were best explained by water temperature and regional discharge. Catch was highest when water temperatures were also high and discharge was low, with most smolts outmigrating when river temperatures were between 3-4°C. The timing of the start of the smolt outmigration period was negatively related to sea surface temperature (SST) in Auke Bay (AMB). The timing of the mid and end points of the smolt outmigration were positively related to smolt length. In the third chapter, the importance of biological and environment factors for explaining annual variation in marine survival was evaluated for Chilkat and Stikine River Chinook Salmon. Marine survival from the Chilkat River was correlated with the timing of the end of the smolt outmigration period, smolt length, and spring discharge, while marine survival for the Stikine River was correlated to smolt body size.

Reductions in the productivity and abundance of Chinook Salmon stocks throughout SEAK have led to increased stock assessments and reductions in harvest (ADF&G Chinook Salmon Research Team 2013). Although previous research has indicated that size-selective pressures in freshwater and during the first year at sea can determine brood-year (BY) recruitment strength of Pacific salmon, the nature of these relationships for these two regionally important Chinook Salmon stocks was previously unclear (Holtby et al. 1990; Beamish and Mahnken 2001; Mueter et al. 2002; Murphy et al. 2013). In chapters one and three of this research, it was determined that recruitment success of Chinook Salmon from the Chilkat and Stikine rivers was influenced by processes that occurred in the early marine period. These results are consistent with the critical size, critical period hypothesis which proposes that BY survival and recruitment strength is determined by an individual's ability to attain a certain minimum body size before the first fall and winter at sea (Beamish and Mahnken 2001). Fish that do not reach this size threshold die as a result of unmet metabolic requirements that compromise swimming ability and lead to predation or cause starvation (Beamish and Mahnken 2001). Through the identification of critical periods in the life history of these Chinook Salmon stocks, managers can implement more guided and direct management tactics.

The relationship between marine survival and freshwater growth in previous research has been less clear as freshwater growth and smolt body size influence survival in some stocks (Sockeye Salmon *Oncorhynshus nerka*: Koenings et al. 1993; Atlantic Salmon *Salmo salar*: Antonsson et al. 2010), but not others (Chinook Salmon *O. tshawytscha*: Graham 2016). Although freshwater growth was only significantly related to marine survival of Chinook Salmon from the Stikine River, the relationship between freshwater growth and first-year marine growth observed for fish from the Chilkat River indicated that increased freshwater growth and larger smolt body size positively influenced the marine survival for both of these salmon stocks. Increased body size and growth during freshwater residence may have increased survival by reducing size-selective predation and enhancing growth opportunities through less gape-size limitations during the first year at sea.

Prior to the current study, little was known about the dynamics of downstream smolt migration of Pacific salmon in glacial rivers. Previous research suggested that smolt outmigration timing was stock specific and dependent on abiotic factors such as photoperiod, water temperature, and discharge and biotic factors such as smolt body size (Bohlin et al. 1993; McCormick et al. 1998). By analyzing Chinook Salmon smolt catch data from the Chilkat River, general trends were identified in run timing, environmental stimuli of outmigration, and relationships between smolt outmigration timing and marine survival. Smolt outmigration timing has influenced the marine survival of other salmon stocks, where early emigrating smolts had the lowest survival due to colder SSTs and poor forage conditions, which limited growth (Mortensen et al. 2000). In the current study, marine survival was higher in years when the smolt outmigration ended later, which may indicate timing at the end of the smolt outmigration was related to a longer, more favorable marine growing period. A significant relationship was detected between the start of the outmigration period and June-July SST at Auke Bay, where smolt outmigrations started later when SSTs were cooler. This suggests that in-river conditions, correlated to marine temperatures, stimulated the onset of smolt migration. Although this study demonstrated the importance of smolt outmigration timing on marine survival of Chinook Salmon, direct survival advantages based on timing were not identified. This project acts as a baseline analysis that indicates a need for additional, more direct sampling. Previous research on smolt outmigration timing utilized coded-wire-tags (CWT) with unique codes based on early, middle, or late run time and adult return rates to identify survival advantages based on outmigration timing (Mortensen et al. 2000; Antonsson et al. 2010). Because the freshwater and first-year marine rearing periods are critical in determining recruitment strength of Pacific salmon, a better understanding of the transition between these two environments will allow for additional insights into factors influencing recruitment variability and stock declines.

Although this research detected significant relationships between freshwater and first-year marine growth and survival of these two Chinook Salmon stocks, the influence of climate and marine conditions on these relationships remains unclear. The current study indicated that poor growth conditions during the first year at sea impacted survival and recruitment success of Chinook Salmon. Because Chinook Salmon are ectotherms, their environment dictates growth directly through metabolic efficiency and indirectly through prey composition and abundance (Cho et al. 1982; Mueter et al. 2002). In Alaska, warmer coastal SSTs have been linked to increased zooplankton abundances that provide Pacific salmon with an optimum prey base, thereby increasing salmon growth and survival as well (Mortensen et al. 2000; Mueter et al. 2002). In the current study, significant relationships were observed between daily catch and the timing of smolt outmigration and climate variables, including discharge and water temperature. These results indicated that in glacial rivers, cold water temperature, and high discharge was related to higher air temperature and SSTs, which may be the factors that Chinook Salmon smolts responded to and what stimulated migratory behavior in the Chilkat River. Climactic variation and shifts in seasonal transitions have led to match-mismatch situations, where environmental factors stimulated smolts to outmigrate outside of the optimal smolt "window" at which they experienced thermal stress and low food availability. This, in turn, may have reduced growth and reduced survival (Rikardsen et al. 2004; Hvidsten et al. 2009). With climate in the northern regions expected to shift rapidly to warmer and more variable regimes, understanding how climate influences Chinook Salmon growth, migration, and survival will provide managers with additional knowledge on how these regionally important stocks adapt to a changing environment.

Previous research on Chinook Salmon from the Chilkat and Stikine rivers has indicated a shift in age class proportions from relatively equal proportions of age-1.3 and age-1.4 fish to a much larger, unbalanced proportion of age-1.3 fish (B. Elliott and T, Jaecks, ADF&G, unpublished data). Declines in age-class diversity have been correlated to declines in stock resilience through an increase in the number of fish in a cohort that are influenced by unfavorable growth and survival conditions in a given year (Schindler et al. 2010). The reduction in the resilience observed in these Chinook Salmon stocks puts them at increased risk for recruitment failure when met with suboptimal marine conditions imposed by climate change or habitat destruction from mine development and structure failure. The results of the current study provided important insights on how annual growth influenced the survival and recruitment success of two regionally important Chinook Salmon stocks in SEAK. In addition, it presented evidence which demonstrated the importance of migration timing on the marine survival of Chinook Salmon in a glacial river. The results of this study may help improve the accuracy and reliability of forecasts for stocks in this region as it detected strong relationships between marine survival and smolt attributes (i.e., body size and outmigration timing) which are collected as each cohort outmigrates to ocean rearing locations. Future research should focus on smolt outmigration timing and the direct influences of climate on early marine growth and recruitment success of Chinook Salmon stocks in this region.

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